The Cape genus Lachnaea (Thymelaeaceae): a monograph

by

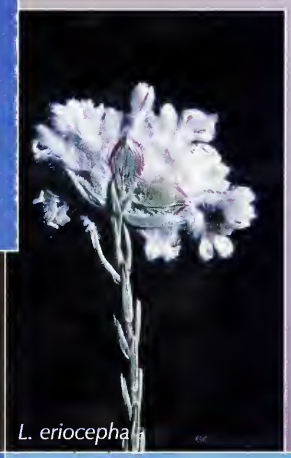
J B P Beyers

L. filamentosa

L. globulifera

L. grandiflora

L. pudens


L. eriocepha

L. pomposa

STRELITZIA 11

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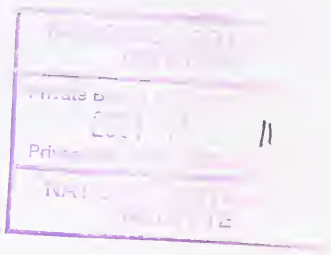
STRELITZIA 11

The Cape genus *Lachnaea* (Thymelaeaceae): a monograph

by

Josephine Bertha Pauline Beyers



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2001

STRELITZIA

This series has replaced *Memoirs of the Botanical Survey of South Africa* and *Annals of Kirstenbosch Botanic Gardens* which the NBI inherited from its predecessor organisations.

The genus *Strelitzia* occurs naturally in the eastern parts of southern Africa. It comprises three arborescent species, known as wild bananas, and two acaulescent species, known as crane flowers or bird-of-paradise flowers. The logo of the National Botanical Institute is based on the striking inflorescence of *Strelitzia reginae*, a native of the Eastern Cape and KwaZulu-Natal that has become a garden favourite worldwide. It symbolises the commitment of the National Botanical Institute to promote the sustainable use, conservation, appreciation and enjoyment of the exceptionally rich plant life of South Africa, for the benefit of all its people.

Cover by Sandra Turck. Flowers on front cover: *Lachnaea eriocephala*, *L. filamentosa*, *L. globulifera*, *L. grandiflora*, *L. pomposa*, *L. pudens*. Back cover: *L. alpina*, *L. filamentosa*, *L. laniflora*, *L. macrantha*.

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Abstract

The circumscription of *Lachnaea* L. (Thymelaeaceae) is extended to include the five species previously placed in *Cryptadenia* Meisn. Four species and all varieties are reduced to synonymy; 12 species are newly described and one new name is proposed. Forty species and two subspecies are now recognized. No formal infrageneric groupings are upheld. Evidence from macromorphology, leaf anatomy, ecology and geographical distribution was used as basis for species delimitation. Palynology and chromosome numbers were found to be taxonomically insignificant at specific level. Two cladistic analyses show that *Lachnaea* is monophyletic and that previously proposed sections are paraphyletic. The two analyses produced mixed resolutions regarding the solitary-flowered species and gave conflicting results with regard to the evolutionary pathway of certain characters. Allopatric speciation appears to have been the dominant process in the evolution of *Lachnaea*. Additional variables that may have governed diversification are altitudinal difference, allochrony and post-fire regeneration strategies.

Lachnaea is endemic to the Cape Floristic Region and occurs almost exclusively in fynbos vegetation. The highest concentration of species (24) is found in the 3319 (Worcester) grid.

The taxonomic treatment includes a brief history of *Lachnaea*, keys to species and subspecies, detailed descriptions with notes on nomenclature, diagnostic features, relationships, distribution, ecology and conservation status. Line drawings and a distribution map are provided for each species.

Keywords: anatomy, conservation, cytology, ecology, morphology, palynology, phylogeny, phytogeography, speciation, systematics

New name, species and subspecies in Strelitzia 11 (2001)

Lachnaea elsieae *Beyers*, sp. nov., 84
Lachnaea globulifera subsp. **incana** *Beyers*, subsp. nov., 105
Lachnaea greytonensis *Beyers*, sp. nov., 89
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1. Introduction

The genus *Lachnaea* L., endemic to the Cape Floristic Region, belongs to the Thymelaeaceae, a medium-sized family comprising about 50 genera and 700 species (Mabberley 1997; Takhtajan 1997). The family is found in both temperate and tropical regions, but is more diverse in the southern than in the northern hemisphere, and is especially well represented in Australia and tropical Africa (Heywood 1979; Mabberley 1997; Takhtajan 1997). Many genera are found on the Pacific Islands (Heywood 1979).

Although relatively homogeneous, the family is usually divided into four subfamilies, namely Gonostyloideae, Aquilarioideae, Synandrodaphnoideae and Thymelaeoideae. The Gonostyloideae and Aquilarioideae have either been treated as separate families or have been included as subfamilies within the Thymelaeaceae (Domke 1934; Hutchinson 1969; Heywood 1979; Cronquist 1981; Mabberley 1997; Takhtajan 1997). The subfamily Gonostyloideae comprises three small genera from Southeast Asia and Borneo, the Aquilarioideae seven small genera from the Pacific area and Africa and the Synandrodaphnoideae one genus, *Synandrodaphne* Gilg, from tropical West Africa (Heywood 1979). Most members of the family are placed in the cosmopolitan Thymelaeoideae.

The taxonomic affinities of the family Thymelaeaceae have been much debated. In the Bentham & Hooker system it is placed in the Daphnales near the Proteaceae and Penaeaceae (Bentham & Hooker 1880). Hutchinson (1959) classified the family in the Thymelaeales with affinities to the Penaeaceae and Nyctaginaceae. He was however, convinced that, wherever the Thymelaeaceae is placed, it should be followed by the Proteaceae (Hutchinson 1969). In the Engler system according to Melchior (1964) it also falls under the Thymelaeales but is placed next to the Dichapetalaceae and Elaeagnaceae. Affinities of the Thymelaeaceae with the Euphorbiaceae are proposed in the Young system (Brummitt 1992) where it is placed in the Euphorbiales, and by Takhtajan (1969 & 1997) who assigned it to the Thymelaeales, adjacent to the Euphorbiales. Dahlgren in his classification of 1975 follows Takhtajan (1969). The former uncertainty regarding the affinities of the family is demonstrated in publications by Thorne (1968, 1976, 1981). In the 1976 version of his classification, he included Thymelaeaceae in the Myrtales, but in a subsequent treatment (1981) he returned it to the Euphorbiales where he had placed it earlier (1968). Cronquist (1981) included Thymelaeaceae in the Myrtales adjacent to Crypteroniaceae and Trapaceae. Dahlgren & Thorne (1984) were of the opinion that Thymelaeaceae does not belong in the Myrtales but that it should be classified near the Euphorbiaceae and that these two families are related to the Malvales. The Angiosperm Phylogeny Group (1998) has included Thymelaeaceae in the Malvales without indicating the families adjacent to it. Nandi *et al.* (1998), in a combined cladistic analysis of angiosperms using *rbc*L and non-molecular data sets, found the Thymelaeaceae to be nested within the Malvales *s.l.* clade. There can be little doubt that the taxonomic affinity as indicated by The Angiosperm Phylogeny Group (1998) and by Nandi *et al.* (1998) is correct.

The southern African members of the Thymelaeaceae all belong to the subfamily Thymelaeoideae. The four genera occurring in the Cape Floristic Region, as defined by Goldblatt & Manning (2000), namely *Gnidia* L., *Lachnaea*, *Passerina* L. and *Struthiola* L., belong to the tribe Gnidieae (Domke 1934). Since Beyers & Van der Walt (1995) concluded that *Lachnaea* and *Cryptadenia* Meisn. are congeneric, the circumscription of *Lachnaea* has been extended to include all five species of *Cryptadenia*. *Lachnaea*, which now consists of 40 species, is endemic to the Cape Floristic Region. *Gnidia,* the largest genus in the Thymelaeaceae, with about 140 species, is mainly an African group (Bredenkamp & Beyers 2000) with approximately one third of the species (49) in the Cape Floristic Region (Goldblatt & Manning 2000). Both *Struthiola* with 42 species (Bredenkamp & Beyers 2000), and *Passerina* with about 20 species (Bredenkamp & Beyers 2000) occur mainly in the Cape Floristic Region.

Lachnaea is poorly known among the general public and flower enthusiasts because most species occur on mountain slopes and summits at high altitudes, usually in relatively small, localized populations. Sometimes these populations are limited to just a few plants. Numerous species, however, with their showy inflorescences and long blooming periods, have great potential for the horticultural industry. Already in the latter half of the eighteenth and beginning of the nineteenth century, four species were cultivated in conservatories in England. These introduced species were propagated by seed and cuttings, and grew best in soil mixtures of peat and loam. At present, however, no member of the genus is commercially available or known to be cultivated in gardens. During this study, numerous attempts were made at propagating species of *Lachnaea* by means of cuttings, but with little success. The hope is expressed that the horticultural potential of these beautiful plants will be acknowledged and that the problems constraining propagation will be solved in the near future.

2. Historical review

The genus *Lachnaea* was established by Linnaeus (1753), based on two species, *L. eriocephala* L. and *L. conglomerata* L. The identity of the latter species, which is known today as *Phylica stipularis* L. (Rhamnaceae), was questioned and excluded in most publications after 1792. *L. eriocephala* is the lectotype species of the genus (Domke 1934). Linnaeus in his *Genera plantarum* (1742) accredits *Lachnaea* to Adriaen van Royen, director of the Hortus Botanicus in Leiden during Linnaeus' residence in Holland between 1735 and 1738 (Wijnands 1983). Whether Van Royen suggested the generic name to Linnaeus or whether Linnaeus saw a specimen of his, remains unknown. No original material of *L. eriocephala* was found. Crantz (1766) included previously described *Passerina* species in his concept of *Lachnaea* and divided the genus into two groups, namely *Lachnaeae* consisting of the above two species, and *Passerinae* comprising eight species. The name *Lachnaea* is derived from the Greek *lachneeis*, meaning woolly, which alludes to the woolly inflorescences of several members of the group.

Lamarck (1792) recognized *L. eriocephala* but excluded *L. conglomerata* from his concept of the genus, and described two new species: *L. buxifolia* Lam. and *L. phylicoides* Lam. In subsequent publications by Salisbury (1808), Sims (1813, 1814a, b), and others, new species were described and illustrated from living material growing in conservatories in Britain.

Meisner (1840) published a detailed taxonomic account of the genus based on Drège's collections, in which some *Gnidia* and *Passerina* species were included. He established three sections: *Sphaeroclinium* Meisn., *Conoclinium* Meisn. and *Microclinium* Meisn., based on the inflorescence structure. Thirteen species and six infraspecific taxa were recognized (Meisner 1840). This treatment of *Lachnaea* was published, with some alterations, in De Candolle's *Prodromus* in which 18 species and 13 infraspecific taxa were dealt with (Meisner 1857).

The revision of *Lachnaea* by Wright (1915) in *Flora capensis* 5,2 has been the standard work up to the present. In this treatment he re-instated *L. purpurea* Andr., which Meisner had regarded as a variety of *L. eriocephala*, and included three new species: *L. funicaulis* Schinz (Schinz 1895), *L. micrantha* Schltr. (Schlechter 1898) and *L. passerinoides* N.E.Br. (Brown 1901), and regarded *L. dubia* Gand. (Gandoger 1913) as an imperfectly known species. Nineteen species and eight infraspecific taxa were included, but no mention was made of the sections established by Meisner. In a subsequent addendum to the *Flora capensis* 5,2 (Wright 1915), Wright (1925) recognized a further two species and two infraspecific taxa which had already been taken up in Meisner's treatment (1857). *Lachnaea marlothii* Schltr. (Schlechter 1896) and *Lachnaea gracilis* Meisn. (Meisner 1840) were both overlooked by Wright.

Between 1934 and 1953 four new species were described, namely *L. elegans* Compton (Compton 1934a), *L. glomerata* Fourc. (Fourcade 1934), *L. naviculifolia* Compton (Compton 1934b) and *L. ruscifolia* Compton (Compton 1953). Thoday (1924) noted in his revision of the genus *Passerina* that the type of *Passerina laniflora* C.H.Wright was not a *Passerina* but a species of *Lachnaea*. Bond (1982) proposed the new combination, *Lachnaea laniflora* (C.H.Wright) Bond. Van Wyk (1993) recognized 29 species. Recently two new species have been described, namely *L. pudens* Beyers (Beyers & Van Wyk 1998a) and *L. sociorum* Beyers (Beyers & Van Wyk 1998b).

The genus *Cryptadenia*, with five species, was established by Meisner (1840) and was also based on Drège's collections. Meisner (1840) regarded the glands (floral scales) which are positioned much lower down in the hypanthium, just above the ovary, and the conspicuous filaments which are adnate to the hypanthium, as the main distinguishing characters between *Cryptadenia* and the closely related *Lachnaea*. In De Candolle's *Prodromus* the same five species were recognized by Meisner (1857). The most recent taxonomic treatment of the genus was that of Wright (1915) in *Flora capensis*. He upheld four of the species in Meisner's treatment, reduced *C. ciliata* Meisn. to synonymy under *C. uniflora* (L.) Meisn., and described a new species: *C. laxa* C.H.Wright. Wright (1915) regarded the flowers of *Cryptadenia* as axillary and solitary, and those of *Lachnaea* as terminal, capitate or rarely solitary. Contrary to the criterion he used elsewhere, he described the flowers of *C. laxa* as terminal and solitary! These five species were also recognized by Van Wyk (1993). Beyers & Van der Walt (1995) investigated the generic status of *Lachnaea* and *Cryptadenia* and found no distinguishing characters at generic level to support the separation of the two genera. They therefore proposed that *Cryptadenia* be combined with *Lachnaea*. The necessary nomenclatural changes were provided by Beyers (1997). Four species were transferred to *Lachnaea*, and *C. breviflora* Meisn. was placed in synonymy under *L. grandiflora* (L.f.) Baill.

The name *Cryptadenia* is derived from the Greek *kruptos* (concealed) and *aden* (a gland), and alludes to the fact that the floral scales are enclosed within the hypanthium.

3. Material and methods

MATERIAL

This study is based on an examination of herbarium material and observations made in the field. Live material of 35 of the 41 taxa was studied. Attempts were made to propagate plants from cuttings collected in the wild for cytological investigation, but these were unsuccessful. Fresh material was preserved in formalin-acetic acid-alcohol (FAA) and a voucher herbarium specimen of each collection was made and is housed in the Compton Herbarium (NBG). Material from the following herbaria was studied (abbreviations according to Holmgren *et al.* 1990): BOL, G-DEL (photographs), GRA, K, LINN (microfiches, photographs and photocopies), LY, NBG, NY, P, P-LA (microfiches, photographs and photocopies), PRE, S, SAM, SBT (photocopies), UPS-THUNB (microfiches, photographs and photocopies) and Z.

METHODS

Descriptive terminology follows Stearn (1973) and Radford *et al.* (1974) unless otherwise stated.

Flowers of both fresh material and herbarium material were examined with the aid of a stereomicroscope. Flowers of herbarium specimens were rehydrated in boiling water before being examined. Drawings were made with the aid of a drawing tube; these were used to take measurements of the different floral parts. The length of the hypanthium was measured from the base of the anterior sepal to the base of the hypanthium.

To ascertain whether the floral scales are nectariferous or functioning as osmophores, neutral red stain in distilled water (1:10 000) was used. The entire inflorescence was submerged in the solution for 2–3 hours and then examined under a microscope. The appearance of red spots on the surface of the scales was interpreted as a positive reaction (Kearns & Inouye 1993). Flowers preserved in formalin-acetic acid-alcohol (FAA) were dissected to expose the floral scales. The samples were critical point-dried, thereafter mounted on stubs, coated with gold and studied with a Joel scanning electron microscope (SEM).

For the anatomical study of foliage leaves, both material preserved in FAA and herbarium specimens were used. Herbarium material was rehydrated by placing it in distilled water and heating it slowly to boiling point in a waterbath for approximately one hour, before allowing it to cool. These specimens were then fixed in FAA for at least 48 hours. The preserved material was dehydrated and embedded in wax according to the tertiary butyl-method (Johansen 1940). Transverse sections, 12 µm thick, were cut with a rotary microtome and stained with alcian green-safranin (Joel 1983). For the study of leaf surfaces portions of the leaf blade obtained from herbarium material were mounted on stubs, coated with gold and studied with a Joel scanning electron microscope (SEM). Epidermal cell patterns of the leaf blade were studied under a light microscope after the adaxial and abaxial epidermal layers had been pealed off and then mounted in water.

For chromosome studies inflorescences were fixed in Carnoy's (1886) fixative in the field. After 24 hours, the fixative was replaced with 85% ethanol for 15 minutes and then finally replaced with 70% ethanol. Flower buds were stained in Snow's (1963) fluid. The anthers were removed and squashed in 45% acetic acid.

The HENNIG86 package of programs for parsimony analysis (Farris 1988) was used for the cladistic analyses. CLADOS (Nixon 1993) was used to look at character distribution on the HENNIG trees.

The conservation status of each taxon was established according to the IUCN Red List Categories and criteria (Walter & Gillett 1998).

CITATION OF LITERATURE, SPECIMENS AND AUTHORS

Titles of books are abbreviated as in *Taxonomic literature*, edn 2 (Stafleu & Cowan 1976–1988). Author citations follow Brummitt & Powell (1992).

Ecklon and Zeyher's collections are cited using the Drège (1847a) code system when definite collecting numbers are unavailable. These numbers are not collection numbers but refer to the numbering system for localities visited by Ecklon and Zeyher, together with the month during which the locality was visited. Ecklon and Zeyher numbers should therefore be interpreted as collections without numbers, for example '*Ecklon & Zeyher s.n. 52.2*'.

Geographical distribution is reflected in accordance with the grid reference system of Edwards & Leistner (1971).

TAXONOMIC CONCEPTS

Luckow (1995) and McDade (1995) highlighted the importance of explicitly stating the concepts and methods used for recognition of taxa in botanical monographs. In the treatment of the monophyletic genus *Lachnaea*, the species delimitation is mainly based on macromorphological, anatomical and geographical char-

acters. The units recognized here should be referred to as 'taxonomic species' (Cronquist 1978; Grant 1981) rather than biological species as defined by (Grant 1981). The species are not based on single characters but on a combination of characters unique to them. Subspecific entities have been used in only one species: *L. globulifera*, because the taxa are allopatric and distinguished only by two characters.

4. Taxonomic significance of characters

In existing taxonomic treatments of *Lachnaea* (Meisner 1840, 1857; Wright 1915) attention was given to macromorphological characters observed solely from herbarium specimens to delimit the species. In order to provide an empirical basis for a revised infrageneric classification of *Lachnaea* and to find new criteria for defining more natural groups, an analysis of all the species was necessary. In the present study the growth habit, morphology of the leaves, inflorescences and flowers, anatomy of the leaves, pollen morphology and the chromosome numbers were examined. As Stace (1989) states: 'Any data which show differences from species to species are of taxonomic significance, and thus constitute part of the information or evidence which may be used by taxonomists'. In this chapter each potential source of taxonomic evidence is dealt with in a short introduction, followed by the variation observed in *Lachnaea* and the taxonomic relevance of the particular feature.

4.1 HABIT

The Thymelaeaceae are shrublets, shrubs or small trees (Domke 1934; Bredenkamp & Beyers 2000). In past taxonomic treatments of *Lachnaea* (Meisner 1840, 1857; Wright 1915) little emphasis was placed on habit. No information was given, for example, on the regeneration of the species. Wright (1915), in the key to the species, used the following as diagnostic features: branch length (short or long), presence or absence of pubescence, and whether branches are straight or flexuous.

Observations

All *Lachnaea* species are shrubs or shrublets varying in height from 0.3–2.0 m. The branching system is markedly sympodial in most species, but often rather irregular, especially in those with alternate leaves. There is considerable variation in appearance and size among and sometimes within the different species. The habit is very variable: erect, sparsely to moderately branched shrubs up to about 2.0 m tall, as in *L. capitata* and *L. macrantha*; erect or straggling, moderately branched shrublets of about 0.3 m tall, as in *L. burchellii* and *L. laxa*; or dense, much-branched, compact, round shrubs up to 1.0 m high, as in *L. alpina*. Within some species the height is very variable: in *L. filamentosa* it varies from 0.3–2.0 m. Individuals growing in moist places grow more luxuriously than those on drier sandy habitats (Table 1).

Species are either basally single-stemmed reseeders, as in *L. densiflora*, or basally multistemmed resprouters, as in *L. axillaris*, or species may be both single- and multistemmed, as *L. filamentosa*, *L. burchellii* and *L. aurea*. Resprouting individuals can usually be distinguished from reseeding ones by their more rounded and compact form (Table 1).

The general appearance of some species may change considerably if grazed by livestock. In both *L. gracilis* and *L. elsieae* grazed individuals are very compact shrublets differing considerably from ungrazed ones.

Some species have rigid, moderately stout branches, as in *L. pomposa*, whereas others have lax or flexuous, slender branches, as in *L. gracilis* and *L. burchellii*. The branches are at first leafy, glabrous or variously pubescent, either terete or ridged below the leaf bases. Older branches become defoliated, glabrous and in many species marked with more or less conspicuous leaf scars (Table 1). Trichomes, which may be present on many parts of the plant, are always unicellular and unbranched.

Discussion

There is considerable infraspecific variability in height and general appearance in some species, especially when individuals are both reseeders and resprouters, or when they have been grazed, whereas other species do not show great variability. In the latter case the habit and size, in combination with other characters, can be of taxonomic value. Similarly, the regeneration strategy is of taxonomic value if it is constant within a species. The presence or absence and the kind of indumentum, and whether the branches are terete or ridged below the leaf base are also taxonomically significant.

4.2 LEAF MORPHOLOGY

In Thymelaeaceae the leaves are always simple, entire, exstipulate, sessile or subpetiolate, either alternate or opposite (Domke 1934). The phyllotaxis may be constant within a genus or a species but may sometimes differ within an individual (Domke 1934). Meisner (1840, 1857) based his sections and subsections mainly on inflorescence morphology, and used phyllotaxis, arrangement and leaf shape as secondary characters. In section *Sphaerocliniium*, Meisner (1840) distinguished two groups. In the first one, with capitula without an involu-

TABLE 1.—Regeneration, height of plant and selected branch characters of *Lachnaea* species

Species	Regeneration		Maximum height in m	Selected branch characters																
							Indumentum													
	reseeder	resprouter		ridged below leaf base	terete	leaf scars	glabrous	hirsute	sericeous-hirtellous	sericeous	sericeous-tomentose	villous-tomentose	tomentose	felted	adpressed hairy	straight hairs admixed crisped ones	short crisped hairs	short straight hairs	glabrescent
alpina	×		1	×		❖	×	†											
aurea		×	1	×		❖									×				
axillaris		×	0.75		×	❖				×	×								
burchellii	×		0.3	×		❖	×								+				
capitata	×		1.8	×		❖	×			†									
densiflora	×		0.5	×		❖				×	×								
diosmoides	×		1.5	×		❖	×												
elsieae	×	×	0.6		×	0						×		×					
ericoides	×		0.5	×		❖										×			
eriocephala	×		0.6		×	0			×										
filamentosa	×	×	2	×	×	❖	×												
filicaulis		×	0.4	×		0				×									
funicaulis	×		0.45		×	0								×					
globulifera																			
subsp. *globulifera*	×		0.6(–0.9)		×	0											×		
subsp. *incana*		×	0.3–0.6(–1.0)		×	0								×					
glomerata		×	0.45	×		❖	×								+				
gracilis	×		2	×		0									+				
grandiflora		×	0.2–0.6(–1.0)	×		❖									×				×
greytonensis	×		0.45		×	0								×					
laniflora	×		1		×	❖							×						
laxa	×		0.3	×		0				×									
leipoldtii	×		0.4		×	0							×						
macrantha	×		2	×		❖	×												
marlothii	?	?	0.3		×	0							+	×					
montana	×		0.6		×	0											×	×	
naviculifolia		×	1.5		×	❖	×			†					×				
nervosa	×	×	1	×		0				+									
oliverorum	×		0.5		×	0								×					
pedicellata	×		0.6		×	0											×	×	
pendula	×		0.45		×	0								×		×			
penicillata	×	×	0.4		×	0								×					
pomposa	×	×	1.7	×		❖	×								†				
pudens	×		0.6	×		❖							×						
pusilla	×		0.4		×	0				×									
rupestris	×		0.2		×	0										×			
ruscifolia		×	0.8	×		❖										×			
sociorum		×	0.6	×		❖										×			
stokoei	?	?	?	×		❖										×			
striata		×	0.6	×		❖				+									
uniflora	×	×	0.45	×		❖	×			✳					+				
villosa	×		0.5		×	0								×					

✳ occasional occurrence; + sparse indumentum; † distal 1–6 internodes; ❖ prominent; 0 inconspicuous.

cre, referred to as subsection *Exinvolucratae* by Meisner (1857), the leaves are alternate, close together, rather broad and flat. In the second group, with capitula possessing an involucre (Meisner 1840), and designated subsection *Involucratae* by Meisner (1857), the leaves are decussate, rarely alternate, linear and dorsally convex or keeled. In section *Conoclinium* the leaves are alternate and semispreading (Meisner 1840 & 1857), whereas in section *Microclinium* the leaves are alternate or opposite, linear or almost needle-shaped (Meisner 1840 &1857). Macromorphological leaf characters were used frequently in Wright's (1915) key to the species of *Lachnaea*.

Observations

In *Lachnaea* the leaves are either alternate or decussate, only in *L. burchellii* are they decussate or occasionally subopposite. The orientation and position of the leaves on the axis are variable among and within species. The leaves are imbricate to scattered, adpressed, subadpressed, ascending, patent, or only very occasionally reflexed (Table 2). The leaves are always entire and usually sessile, but may be subpetiolate as in *L. ruscifolia*.

Leaf shape varies from linear to orbicular. Again the variability is not only interspecific but also infraspecific and is found even on the same individual. In *L. pom-*

TABLE 2.—Leaf characters (phyllotaxy, orientation, structure, shape, size) in *Lachnaea* species

Species	Phyllotaxy			Orientation						Structure		Shape									Size	
	alternate	sub-opposite	decussate	adpressed	subadpressed	ascending	inclined	patent	reclined	amphistomatic	epistomatic	linear	lanceolate	narrowly elliptic	narrowly ovate	narrowly obovate	elliptic	ovate	obovate	widely ovate	orbicular	length (mm)	width (mm)
alpina	×					×					×			×			×		×			5–10	1.5–3
aurea	×			×	×	×		✳	✳		×			×			×		×			7.5–18	0.8–4
axillaris			×			×					×		×		×							2–4	0.8–1.2
burchellii		✳	×			×	×				×		×	×								6–13	1.0–3
capitata	×					×				×		×		×								5.2–21	0.7–1.8
densiflora	×					×	×			×		×		×								5–12(–20)	0.7–2.5
diosmoides	×					×	×	×	✳		×	×		×								5–10	1.0–1.5
elsieae			×	×	×						×		×	×			×	×				1–4.5	0.4–1.1
ericoides	×				×	×					×			×			×		×			2–6(–8)	0.8–1.5
eriocephala			×		×	×					×		×	×								5.2–15	1–2.5
filamentosa	×					×	×	×		×				×	×	×	×	✳	×			7–40	2–13
filicaulis			×			×	×	×			×		×									3.6–8.0(–12.0)	0.6–1–1.5✳
funicaulis			×	×							×		×	×		×						3.8–5	0.8–1.4
globulifera																							
subsp. *globulifera*			×	×	×	×					×			×								5.4–12	0.7–1.7
subsp. *incana*			×	×	×	×					×		×	×								4.5–7.3	0.9–1.7
glomerata			×			×	×	×			×			×			×		×			4–10.5	1–2
gracilis			×	×	×	×					×			×		×	×		×			(3.1–)3.5–8.3	0.8–1.5–3✳
grandiflora			×		×	×					×			×	×	×	×	×				2.2–11.5	0.8–3
greytonensis			×	×							×			×								2.8–4.5	0.8–1.2
laniflora			×			×					×			×	×							2.5–7	0.9–1.3
laxa			×	×	×	×					×		×	×								3.8–7.6	0.6–1.3
leipoldtii			×	×							×			×			×	×				2.2–3.5	0.8–1.2
macrantha	×					×					×								×			7–23	2.9–11
marlothii			×	×	×	×					×			×								2.5–4.2	0.6–1.0
montana			×	×	×	×					×		×	×								4.2–15	1–2.4
naviculifolia			×			×					×			×	✳		×	✳				1.5–16	1.5–5.5
nervosa	×					×	×	×			×			×		✳						4.7–14	0.7–1.5
oliverorum			×	×	×	×					×		×	×								3.8–5	0.8–1.4
pedicellata			×	×	×	×					×	×		×								4.5–12	0.8–1.5
pendula			×	×							×			×	×		×	×				1.8–2.4	0.6–0.8
penicillata			×	×							×		×	×								2–3.7	0.6–1
pomposa	×					×	×	×	✳	×				×	×	×	×	×	×	×		7–38	2–19
pudens			×			×					×						×					3.8–5	1–1.3
pusilla			×	×							×			×								2.8–3.2	0.6–0.7
rupestris			×		×	×					×		×	×								3–5.4	0.6–1
ruscifolia	×					×	×	×			×							×			×	5–10.5	2.6–5.5
sociorum	×					×	✳	✳			×		×	×			✳		✳			3.6–6	0.9–2.4
stokoei	×					×					×			×			×	×				2.5–4	1–1.5
striata	×					×					×			×			×	×				4.8–10	1.5–4.5
uniflora			×	×	×	×					×		×	×								3.4–6.7	0.6–1
villosa			×	×							×		×	×								2.8–5	0.6–1.2

✳ occasional occurrence.

posa, for example, leaves may vary from narrowly elliptic to elliptic, narrowly ovate to widely ovate and narrowly obovate to obovate on the same plant. Leaf size ranges from 1–40 mm in length and 0.4–19 mm in width. The variation can be considerable within a species, as observed in *L. filamentosa*, with a range of 7–40 mm long and 2–13 mm wide and in *L. pomposa* from 7–38 mm long and 2–19 mm wide (Table 2).

The leaf blade varies from more or less plane on both sides to concave adaxially and convex abaxially (Table 3). Abaxially, leaves may be flat or subkeeled to keeled

TABLE 3.—Selected macromorphological leaf characters (shape of lamina as seen in cross section, surface of lamina, indumentum of margin and apex) in *Lachnaea*

Species	Amphistomatic	Shape (cross section)					Surface						Margin				Apex
		adaxial			abaxial		abaxial						indumentum				
		plane	concave	convex	plane	convex	enervate	faintly nervate	subkeeled	keeled	midribbed	mid- & laterally ribbed (quantity)	glabrous	ciliate	lanate	villous	tuft of hairs
alpina		×			×		×						×				
aurea		×			×		×						×				
axillaris		×	×			×	×						×				
burchellii			×		×						×	(3)	×				
capitata	×	×				×	×		✳				×				
densiflora	×	×		×		×	×		✳				×	✳			✳
diosmoides		×				×					×		×				
elsieae			×			×			×	×			×				×
ericoides			×			×				×			×				×
eriocephala			×			×				×				×			
filamentosa	×	×			×		×	×					×				
filicaulis			×			×	×						×				
funicaulis			×			×	×		×						×		
globulifera																	
subsp. *globulifera*			×			×			×				×	✳			
subsp. *incana*		×	×			×			×				×	✳			
glomerata			×			×	×		×				×				
gracilis		×	×		×	×	×						×				
grandiflora			×			×			×				×				
greytonensis			×			×	×		×							×	
laniflora			×			×			×				×				
laxa			×			×	×			×			×				
leipoldtii			×			×				×			×				
macrantha		×			×		×						×				
marlothii			×			×			×				×				
montana		×	×			×				×			×				
naviculifolia		×				×	×						×				
nervosa		×	×			×					×	(3–5)	×				
oliverorum			×			×	×		×						×		
pedicellata			×			×				×			×				
pendula			×			×	×		×				×				×
penicillata			×			×			×	×					×		×
pomposa	×	×			×		×	×					×				
pudens			×			×				×			×				
pusilla			×			×			×				×				
rupestris			×			×			×				×				
ruscifolia			×			×						(6–9)		×			
sociorum		×	×			×			×			+(3)	×				
stokoei			×		×			×					×				×
striata		×			×						×	(3–5)		×			
uniflora			×			×			×				×				
villosa			×			×			×	×					×		

✳ occasional occurrence; + less pronounced.

TABLE 4.—Vouchers of material studied for leaf anatomy and chromosome numbers in *Lachnaea*. All housed at NBG except where otherwise stated

Species	Voucher specimen	Transections	Surfaces: SEM	Chromosome no. (2n)
alpina	*Beyers 258*	×		
	Forsyth 508		×	
	Oliver 9299	×	×	18
aurea	*Beyers 135*	×	×	
axillaris	*Beyers 127*	×		
	Beyers 180	×	×	
	Schlechter 7702 (BOL)	×		
burchellii	*Oliver 9241*	×	×	
	Oliver 9251	×	×	
capitata	*Beyers 138*	×	×	
	Oliver 10519			18
densiflora	*Beyers 115*	×		
	Beyers 145	×	×	18
	Beyers 171	×		
	Beyers 177		×	
diosmoides	*Beyers 181*	×	×	18
	Spreeth 158		×	
elsieae	*Hanekom 3013*	×	×	
	Taylor 10751	×		
ericoides	*Beyers 172*	×	×	18
eriocephala	*Beyers 54*	×	×	18
	Esterhuysen 18794		×	
	Rugge s.n.			18
filamentosa	*Beyers 110*	×	×	
	Hansford 47	×		
	Low 1246		×	
	Taylor 10770		×	
filicaulis	*Boucher 5071*	×	×	
	McDonald 1989			18
	Oliver 9803	×		
funicaulis	*Bolus 5316*	×		
	Hugo 2332	×	×	
globulifera				
subsp. *globulifera*	*Beyers 240*	×	×	
subsp. *incana*	*Brown 575*	×	×	18
glomerata	*Beyers 129*	×	×	18
	Vlok 2378	×	×	18
gracilis	*Bean & Viviers 2613*		×	
	Beyers 126		×	
	Beyers 219	×		
	Marloth 3224 (BOL)		×	
	Oliver 10415	×	×	
	Oliver 10416			18
grandiflora	*Beyers 129*	×	×	
	Beyers 151	×		
	Beyers 155		×	
greytonensis	*Beyers 209*	×	×	
laniflora	*Forsyth 507*	×	×	18
	Hanekom 667	×	×	
	Oliver 9045	×	×	
laxa	*Bolus 7875* (BOL)	×	×	
	Oliver, 1 4	×		
leipoldtii	*Taylor 10871*	×	×	
macrantha	*Forsyth 527*	×	×	
	Oliver, I. 3	×	×	18
marlothii	*Kotze 124*	×		
	Phillips 2051 (SAM)	×	×	
montana	*Beyers 141*	×	×	18
	Beyers 276	×		
naviculifolia	*Beyers 114*	×	×	
	Forsyth 525		×	
nervosa	*Beyers 215*		×	
	De Kock 152	×	×	
	Esterhuysen 36180		×	
	Oliver 9259	×	×	18
oliverorum	*Oliver 10478*	×	×	
	Viviers & Vlok 430	×		
	Williams 1195		×	
pedicellata	*Oliver 9282*	×	×	
pendula	*Esterhuysen 29780* (BOL)	×	×	
	Esterhuysen 30420 (BOL)		×	
penicillata	*Beyers 173*	×	×	
	Oliver & Fellingham 9145		×	
pomposa	*Beyers 122*	×	×	18
	Compton 21088		×	
pudens	*Beyers 161*	×	×	
	Beyers 166	×		
	Beyers 210	×	×	
pusilla	*Beyers 243*	×	×	
	De Villiers 45		×	
rupestris	*Oliver s. n.*	×	×	
ruscifolia	*Beyers 193*		×	
	Vlok 2084	×	×	
	Goldblatt & Manning 8870	×		
sociorum	*Beyers 176*	×	×	18
	McDonald 2059	×	×	
stokoei	*Stokoe NBG 103641*	×	×	
striata	*Esterhuysen 26861* (BOL)		×	
	Leipoldt 3504 (BOL)	×		
	Stokoe BOL 22326	×		
uniflora	*Beyers 136*	×	×	18
villosa	*Beyers 125*	×	×	
	Du Toit s.n.			18
	Oliver 9808			18

in the distal half, or enervate to longitudinally 1–9-ribbed. Both surfaces are usually smooth but in *L. grandiflora* the abaxial surface may be transversely rugose towards the margins. The adaxial side is usually enervate, only occasionally midveined or subnervate as in *L. pomposa*. The abaxial surface is usually green, glossy and smooth, whereas the adaxial surface is usually pale green, dull and white-punctulate. Leaves are concolorous in *L. capitata*, *L. densiflora*, *L. filamentosa* and *L. pomposa*, and glaucous in *L. macrantha*, *L. pomposa*, and usually in *L. filamentosa*.

The leaves are coriaceous in most species, but occasionally semisucculent in *L. densiflora* and *L. naviculifolia*. They are mostly glabrous or occasionally ciliate at the margins, or with a tuft of hair at the apex although the latter hairs are often deciduous (Table 3).

The bract-like leaves subtending the inflorescences are discussed under the inflorescences.

Discussion

The following characters were found to be taxonomically relevant: phyllotaxis and to a lesser degree the orientation, shape (in outline and cross section) of the leaves; the abaxial leaf surface, whether enervate or ribbed; the presence or absence and the type of indumentum at the leaf margins. The wider the range of infraspecific variation of a character, the lower its significance to taxonomy.

There are leaf types in *Lachnaea* very similar to those of unrelated groups, as illustrated in *Cliffortia* (Rosaceae) and *Aspalathus* (Fabaceae) in Dahlgren (1971: figs 1–4), and those in the *Relhania* (Asteraceae) revision by Bremer (1976). These convergent similarities are not restricted only to leaf shape. In three *Relhania* species for example the leaves have several parallel ribs (Bremer 1976) as in *L. striata* and *L. ruscifolia*. Fibre bundles running along the leaf margins, as in *L. aurea* and *L. striata*, were also found in many of the *Relhania* species (Bremer 1976). The similarities discussed above are yet more examples of convergent evolution in leaves of especially the flora of the Cape Floristic Region (Went 1971).

4.3 LEAF ANATOMY

Data from comparative plant anatomy are widely used in taxonomic research although they have generally been found more useful in the classification of higher categories. While leaves respond readily to evolutionary pressures towards xeromorphy or other modifications, their endomorphic characters commonly retain the ground plan of the phylad to which they belong (Keating 1984). Metcalfe & Chalk (1950) gave a general description of the leaf anatomy of the Thymelaeaceae. Thoday (1921) alluded to certain aspects of the leaf anatomy of two Cape species of *Passerina*. Beyers & Van der Walt (1995), in their generic delimitation of *Lachnaea* and *Cryptadenia*, give an account of the leaf anatomy of 18 species. In an attempt to determine anatomical and morphological adaptations in the leaves of selected fynbos species, Van der Merwe (1992) gave detailed descriptions of the anatomy of the leaves of two *Passerina* and two *Struthiola* species. Since no attention has been given to the leaf anatomy in past taxonomic treatments of *Lachnaea* (Meisner 1840, 1857; Wright 1915), the taxonomic value of these characters was hitherto unknown. The material used in the leaf anatomical study is tabulated in Table 4.

Observations

Based on structure, two leaf types can be distinguished in *Lachnaea*. Type A: leaves amphistomatic and isobilateral; Type B: leaves epistomatic and dorsiventral.

Type A: Amphistomatic, isobilateral leaves (Tables 3; 5; 6)

In cross section the leaves are either flattened ad- and abaxially, transversely elliptic or flattened adaxially and convex abaxially. The cuticle is well developed and equally thick ad- and abaxially. The cuticular relief, as observed with the SEM, is adaxially undulate, reticulate or depressed reticulate, whereas abaxially it is more or less smooth, reticulate or depressed reticulate (Figure 1). Epicuticular wax deposits (Figure 2) occur on both surfaces. On the adaxial surface the wax deposits are in the form of entire platelets (terminology after Barthlott *et al.* 1998), whereas on the abaxial surface they are either in the form of entire platelets or a crust. The epidermis is uniseriate. Epidermal cells are square to periclinally elongated, more or less the same size ad- and abaxially, with the outer tangential cell walls slightly thicker than the inner ones (before gelatinization). The inner tangential cell walls are ad- and abaxially either partly gelatinized as in *L. densiflora* (Figure 3A) or wholly gelatinized as in *L. pomposa* (Figure 3C). Stomata are anomocytic, more abundant adaxially, and sunken.

The mesophyll is not differentiated into palisade and spongy parenchyma but consists of 6 or 7 layers of palisade-like chlorenchyma. In *L. filamentosa*, however, the chlorenchyma consists of palisade-like cells admixed with rounded cells. Substomatal air chambers are present below the ad- and abaxial epidermis.

The vascular bundles are collateral, consisting usually of one large mid-bundle flanked by one or two smaller bundles on either side with very small intermediate bundles occurring between these two types as in *L. densiflora* (Figure 3A). In this type the mid- and lateral bundles are capped abaxially by large extraxylary fibres, which are particularly well developed in the mid- and lateral bundles. A uniseriate, parenchymatous bundle sheath is present which may be complete as in *L. filamentosa* (Figure 3B) or incomplete and interrupted by the extraxylary fibre cap, as in *L. densiflora*.

Crystals of diosmin (potassium hydroxide test: Jackson & Snowdon 1990) occurring as sphaerocrystalline to somewhat dendritic masses, pale yellow in colour, are present in the epidermis, mesophyll and vascular tissue in *L. filamentosa* and *L. pomposa* (Figure 3B, C). Druse crystals (presumably calcium oxalate) are present in the mesophyll of *L. capitata*, *L. densiflora* and *L. pomposa*. Tanniniferous deposits are absent.

Type B: Epistomatic, dorsiventral leaves (Tables 5–7)

In cross section the leaves are usually flattened to adaxially concave or occasionally transversely elliptic as in *L. laniflora* (Figure 5A), and shallowly to deeply convex abaxially, or flattened ad- and abaxially as in *L. macrantha*. The cuticle is well developed, equally thick ad- and abaxially or thinner adaxially. The cuticular relief, as observed with the SEM, is adaxially more or less smooth, subpapillate to papillate, striate-papillate, depressed reticulate, depressed reticulate-subpapillate or basket-woven. Abaxially the cuticular relief is subpapillate to papillate,

TABLE 5.—Epidermal features of *Lachnaea* species with amphistomatic and epistomatic leaves

Species	Cuticular relief							Epicuticular wax		Stomata		Epidermis cell size			Epidermis cell shape						Tangential cell walls		Inner tangential walls gelatinized					
	adaxial			abaxial											adaxial			abaxial			outer	inner	adaxial			abaxial		
	undulate	reticulate	depressed reticulate	± smooth	reticulate	depressed reticulate		adaxial	abaxial	sunken	level	abaxial = adaxial	abaxial < adaxial	abaxial 2× > adaxial	square	periclinally elongated	radially elongated	square	periclinally elongated	radially elongated	ad- & abaxial epid.	only outer wall of adax. epid. thicker	wholly	partly	weakly	wholly	partly	weakly
Amphistomatic																												
capitata		×			×			P	P	×		×			×	×		×	×		+			×			×	
densiflora		×			×			P	P	×		×			×	×		×	×		+			×			×	
filamentosa			×			×		P	C	×		×			×			×			0			×			×	
pomposa	×		×	×		×		P	C	×		×			×	×		×	×		✳		×			×		
Epistomatic																												
alpina										×		×			×	×		×	×		✳			×		×		
aurea										×		×			×	×		×	×		✳				×	×		
axillaris										×				×	×			×		×	+				×		×	
burchellii										×			×		×	×		×			0				×		×	×
densiflora										×		×			×	×		×	×		+			×			×	
diosmoides										×			×			×		×	×		+			×			×	
elsieae										×				×		×				×		×		×	×	×		
ericoides										×				×	×	×		×		×	+				×		×	
eriocephala										×				×		×		×	×		✳			×	×	×		
filicaulis										×		×			×	×		×		×	0			×		×		
funicaulis										×				×		×				×		×				×		
globulifera																												
subsp. *globulifera*										×				×	×	×		×		×	✳				×	×		
subsp. *incana*										×				×	×	×		×		×	✳				×	×		
glomerata										×				×	×	×		×		×		×			×	×	×	
gracilis										×				×	×	×		×		×	✳				×	×		
grandiflora										×				×	×					×	0				0		0	
greytonensis										×				×		×		×		×		×		×		×		
laniflora										×				×	×	×	×			×	+	×		×	0	×	×	×
laxa										×			×			×			×		0			×		×		
leipoldtii											×			×		×				×	0				×		×	
macrantha										×			×		×	×		×	×		0				×			×
marlothii										×				×	×	×				×	0			×		×		
montana										×				×	×	×		×	×		+			×		×		
naviculifolia										×				×	×		×			×	0			×			×	
nervosa										×				×	×	×		×	×		0			×		×	×	
oliverorum										×				×	×	×				×		×		×		×		
pedicellata										×				×	×	×		×		×	+		×		×		×	×
pendula										×				×		×				×	✳			×	×	×		
penicillata											×			×		×				×	0					×		
pudens											×			×	×	×		×	×		+			×		×		
pusilla										×		×				×			×		0				×	×		
rupestris										×				×	×	×				×	+				×	×		
ruscifolia										×		×			×	×		×	×		0			×			×	
sociorum										×				×		×		×		×		×			×		×	
stokoei										×				×		×		×	×		+		×			×		
striata										×		×	×		×	×		×	×		0			×	×		×	×
uniflora										×			×			×			×		+				×	×		
villosa											×			×		×		×		×	0					×		

C, crust; P, platelets; outer: inner, refers to thickness of outer tangential cell walls with relation to inner tangential cell walls of both epidermides; ✳, > 2 × thicker; + slightly thicker; 0 even thickness

TABLE 6.—Histological features of leaf transections of *Lachnaea* species with amphistomatic and epistomatic leaves

Species	Structure		Mesophyll			Vascular bundles			Extraxylary fibres			Bundle sheath		Crystals							Tanniferous deposits			
						mid	lateral							druse	diosmin									
	isobilateral	dorsiventral	undiff. palisade-like chlorench.	palisade layers	spongy chlorenchyma	size	number & size	intermediate	mid-bundle cap	lateral bundle cap prominent	fibre strands along lat. margin	complete	incomplete	mesophyll	adax. epidermis	abax. epidermis	mesophyll	vascular bundle	bundle sheath	extraxylary fibre cap	adax. epidermis	abax. epidermis	mesophyll	bundle sheath
Amphistomatic																								
capitata	×		6–7			M	2b	×	MX				×	×										
densiflora	×		6–7			M	1–2b	×	MX	×			×	×										
filamentosa	×		6–8			M/m	2b / 3B	×	mx			×			×	×	×	×						
pomposa	×		6–7			M	3B	×	mx			×		×	×	×	×	×						
Epistomatic																								
alpina		×		1–2	×	M	2–3b		mx			×			×	×	×	×	×					
aurea		×		1	×	M	1B	×	MX	×	×		×	×								×	×	
axillaris		×		2	×	M	1b	×	MX	×		×	×				×					×	×	
burchellii		×		1	×	M	2b	×	MX	×			×											
diosmoides		×		1	×	M	1b	×	MX	×			×	×								×	×	
elsieae		×		1	×	M	2b*		MX			×		×									×	
ericoides		×		1	×	M	1b	×	MX				×		×				×			×	×	
eriocephala		×		1	×	M	3–4b*		MX			×		×									×	
filicaulis		×		1	×	M	1b	×	MX	×			×	×								×	×	
funicaulis		×		1	×	M	2–3b*		MX			×											×	
globulifera																								
subsp. *globulifera*		×		1	×	M	2–3b*		MX			×		×									×	
subsp. *incana*		×		2	×	M	3–4b*		MX			×		×								×	×	
glomerata		×		1	×	M	1–2b	×	MX	×			×	×								×	×	
gracilis		×		1–2	×	M	1–2b	×	MX	×			×	×	×	×	×							
grandiflora		×		1	×	M	2–3b	+	MX	×		×	×	×	×		×	×			×	×	+	×	
greytonensis		×		1	×	M	2b*		MX			×										×	×	
laniflora		×		1–2	×	M	2b*		MX			×		×								×	×		×
laxa		×		1	×	M	3–4b	×	MX	×			×	×											
leipoldtii		×		1	×	M	2b*		MX				×	×									×		
macrantha		×		1	×	m	3B	×	mx			×		×											
marlothii		×		1	×	M	2b*		MX				×	×									×		
montana		×		2	×	M	3b*		MX			×		×								×	×		
naviculifolia		×		2	×	M	2–4b*		MX			×		×	×							×	×		
nervosa		×		1–2	×	M	2–3b	×	MX	×			×	×	×		×					+	+		
oliverorum		×		2	×	M	2–3b*		MX			×		×									+		×
pedicellata		×		1	×	M	3b*		MX			×										×	×		
pendula		×		1	×	M	2b*		MX			×											×		
penicillata		×		1	×	M	2b*		MX				×										×		×
pudens		×		1	×	M	2–3b*		MX				×		×	×	×								
pusilla		×		1	×	M	3b*		MX				×												
rupestris		×		1	×	M	2b*		MX			×		×								×	×		×
ruscifolia		×		1	×	m	4–5B	×	MX	×			×		×	×	×								
sociorum		×		1–2	×	M	2b	×	MX	×			×		×		×					×	×		
stokoei		×		1	×	M	2b		MX	×			×	×	×		×					×	×		
striata		×		1	×	M	2b	×	MX	×	×		×	×											
uniflora		×		1	×	M	2–3b	×	MX	×			×	×											
villosa		×		2	×	M	2–4b*		MX			×		×									×		×

+ present or absent; B, same size as mid-bundle; b, smaller than mid-bundle; * very small bundle; M, large; m, small; MX, very well developed; mx, less well developed. Lateral vascular bundle: number refers to number of lateral bundles on either side of mid-bundle.

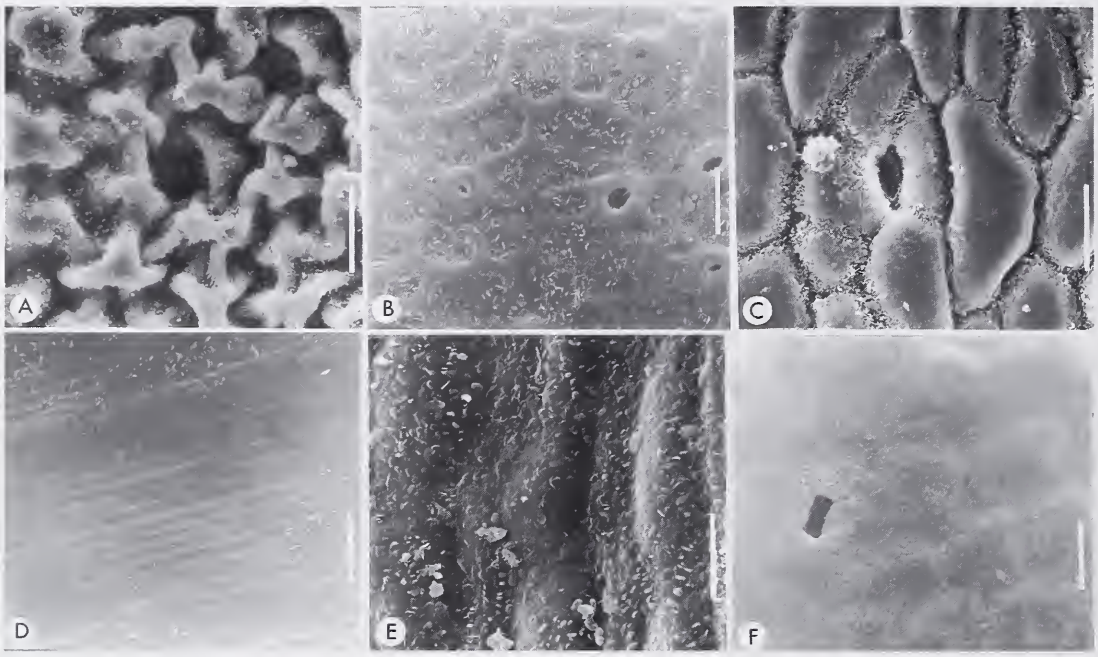

FIGURE 1.—SEM micrographs of cuticular relief in leaves of *Lachnaea* species. A, *L. alpina, Oliver 9299*, adaxial surface, epidermal cells irregularly papillate ('basket woven'); B, *L. capitata, Beyers 138*, abaxial surface, reticulate; C, *L. filamentosa, Taylor 10770*, abaxial surface, areas between epidermal cells depressed reticulate; D, *L. filicaulis, Boucher 5071*, abaxial surface, striate; E, *L. glomerata, Beyers 192*, abaxial surface, undulate; F, *L. pomposa, Beyers 122*, abaxial surface, ± smooth. Scale bars: 37 µm.

striate-papillate, undulate, reticulate, reticulate-subpapillate, striate, depressed reticulate or depressed reticulate-subpapillate (Figures 1; 4). Epicuticular wax deposits occur on both surfaces. These deposits are adaxially usually in the form of platelets, or occasionally in the form of a crust or a smooth layer. On the abaxial surface they appear mostly as a smooth layer with sparse platelets dispersed over the smooth layer, occasionally in the form of a crust, a smooth layer or as platelets, but then the platelets are usually less dense than those found adaxially (Figure 2).

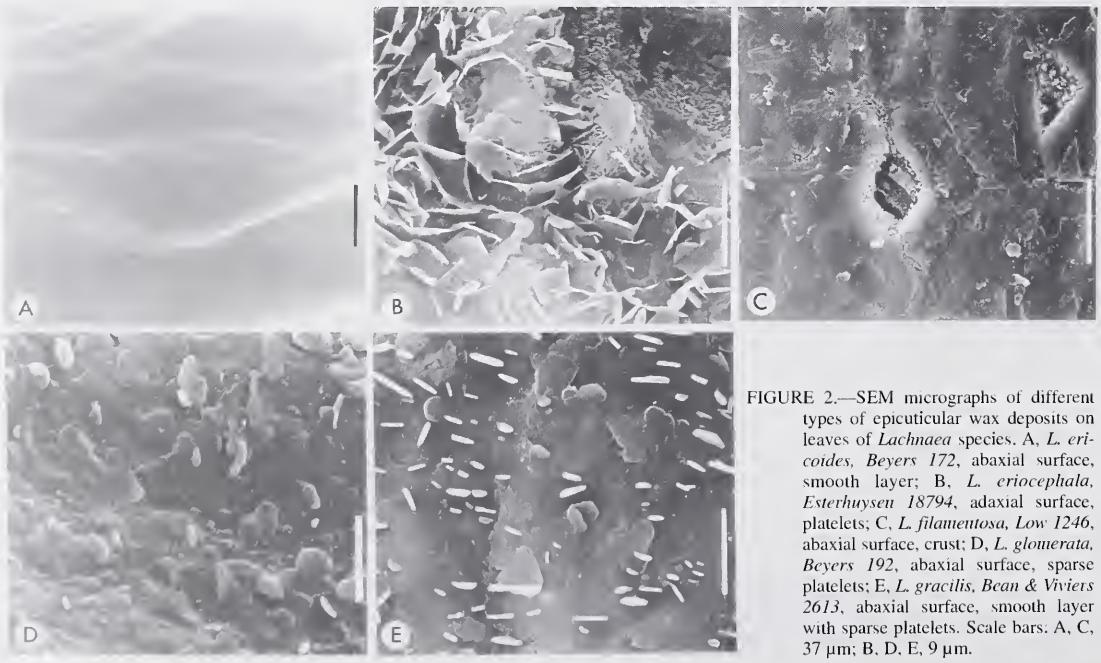

FIGURE 2.—SEM micrographs of different types of epicuticular wax deposits on leaves of *Lachnaea* species. A, *L. ericoides, Beyers 172*, abaxial surface, smooth layer; B, *L. eriocephala, Esterhuysen 18794*, adaxial surface, platelets; C, *L. filamentosa, Low 1246*, abaxial surface, crust; D, *L. glomerata, Beyers 192*, abaxial surface, sparse platelets; E, *L. gracilis, Bean & Viviers 2613*, abaxial surface, smooth layer with sparse platelets. Scale bars: A, C, 37 µm; B, D, E, 9 µm.

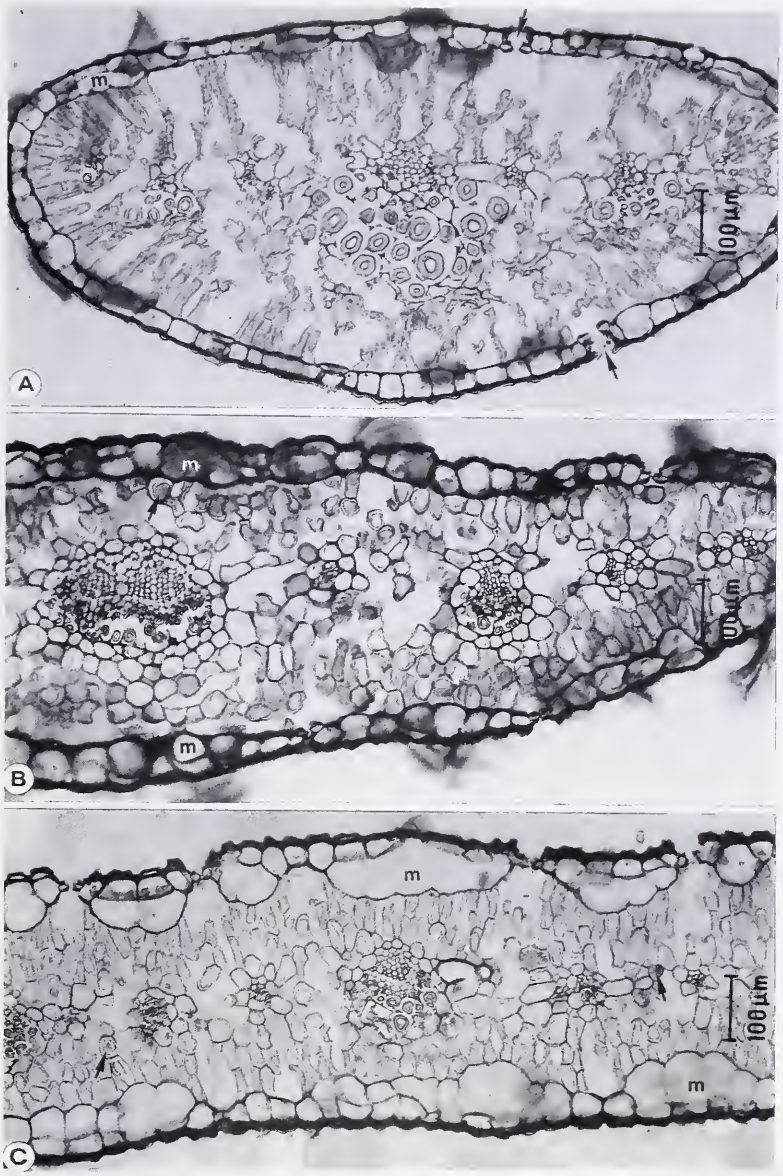

FIGURE 3.—Leaf anatomy in *Lachnaea*: c/s amphistomatic, isobilateral leaves, adaxial face above. A, *L. densiflora*, *Beyers 145*, leaf lamina, note partly gelatinized epidermis with gelatinized (mucilaginous) inner tangential cell walls (m), sunken stomata (arrowed), mid- and lateral vascular bundles with prominent caps of extraxylary fibres. B, C, c/s central portion of leaf: B, *L. filamentosa*, *Beyers 110*, note chlorenchyma consisting of palisade-like cells admixed with rounded cells, complete, uniseriate, parenchymatous bundle sheath and diosmin crystals (arrowed); C, *L. pomposa*, *Beyers 122*, note wholly gelatinized epidermis and the diosmin crystals (arrowed).

Trichomes, when present, are non-glandular and uniseriate. The epidermis is uniseriate. The adaxial epidermal cells are usually much smaller than the abaxial ones (Figure 5), but in a few species they are only slightly smaller or more or less the same size as the abaxial ones. The epidermal cells are either square or periclinally or radially elongated. Before gelatinization of the epidermal walls the outer tangential cell walls of both epidermides are either thicker than the inner tangential cell walls, of even thickness, or in a few species, as in *L. glomerata* (Figure 6A), the outer tangential cell walls of the adaxial epidermis are thicker than the inner walls of the adaxial epidermis and the tangential walls of the abaxial epidermis. The inner tangential cell walls of the adaxial epidermis are either partly to weakly gelatinized or occasionally wholly gelatinized. The inner tangential walls of the abaxial epidermis are usually wholly to partly gelatinized and only occasionally weakly so. The stomata are anomocytic and usually sunken but in three species they occur on the same level as the adjacent epidermal cells.

The mesophyll is differentiated, with palisade tissue occurring abaxially and spongy parenchyma adaxially. The palisade tissue is 1- or 2-seriate. The spongy parenchyma consists of palisade-like cells usually loosely arranged, often with large intercellular spaces.

The vascular bundles are collateral. In some species a large mid-bundle is flanked by one or two, occasionally three or four bundles on either side with very small intermediate bundles occurring between these two types. Each bundle is capped abaxially by large extraxy-

TABLE 7.—Cuticular relief paterns and epicuticular wax in *Lachnaea* species with epistomatic leaves observed under SEM

Species	Cuticular relief																	Epicuticular wax	
	adaxial epidermis							abaxial epidermis										adaxial	abaxial
	± smooth	subpapillate	papillate	striate-papillate	depressed reticulate	depressed reticulate-subpapillate	basket woven	papillate	subpapillate	striate-papillate	undulate	reticulate	reticulate-subpapillate	striate	depressed reticulate	depressed reticulate-subpapillate		
alpina					×		×								×		C	C
aurea			×									×					P	p
axillaris			×													×	P	SL+p
burchellii			×			×										×	P	SL+p
diosmoides			×									×					P	p
elsieae	×															×	C	SL+p
ericoides			×										×				P	SL
eriocephala			×							×			×				P	SL
filicaulis	×													×			P	SL+p
funicaulis	×												×				P	SL+p
globulifera																		
subsp. *globulifera*			×											×			P	SL+p
subsp. *incana*			×										×				P	SL+p
glomerata			×								×		×				P	SL+p
gracilis			×		×										×	×	P	SL+p or P
grandiflora			×						×					×			P	SL
greytonensis			×							×							P	SL+p
laniflora		×	×										×	×			SL or P	SL or SL+p
laxa			×										×				P	SL
leipoldtii				×				×									SL	SL
macrantha			×													×	P	P
marlothii					×				×								P	SL+p
montana			×													×	P	SL+p
naviculifolia			×						×								P	SL or P
nervosa			×									×	×				P	SL+p
oliverorum			×		×								×			×	P	SL+p
pedicellata			×													×	P	SL+p
pendula					×				×						×		C	SL+p
penicillata					×											×	SL	SL+p
pudens			×						×								P	SL+p
pusilla			×			×										×	P	SL+p or p
rupestris			×						×								P	SL+p
ruscifolia			×			×			×	×							P	SL+p or SL
sociorum			×	×				×		×							P	SL+p
stokoei						×							×				P	SL
striata					×						×					×	P	SL+p or SL
uniflora			×													×	P	SL+p
villosa					×											×	SL	SL

C, crust; P, platelets; p, platelets less dense; SL, smooth layer

lary fibres, which are particularly well developed in the mid- and lateral bundles, as in *L. glomerata* (Figure 6A). In *L. ruscifolia* (Figure 6C) and *L. striata* the extraxylary fibre strands of the mid- and larger lateral bundles extend to the abaxial epidermis. The uniseriate, parenchymatous bundle sheath is either complete or, due to the interruption by the extraxylary fibre cap, incomplete. In *L. grandiflora* and *L. ericoides* both states occur. In other species, however, the large mid-bundle is flanked on either side by two to four small to very small bundles without intermediate bundles as in *L. laniflora* (Figure 5A), *L. naviculifolia* (Figure 5B) and *L. pudens* (Beyers & Van Wyk 1998a: fig. 2A). Here only the mid-bundle has abaxially a particularly well-developed extraxylary fibre cap, and the uniseriate, parenchymatous bundle sheath is either complete or incomplete. In *L. leipoldtii* the extraxylary fibre cap is exceptionally well developed and extends to the abaxial epidermis. Extraxylary fibres not associated with the vascular bundles, occur along the lateral margins immediately below

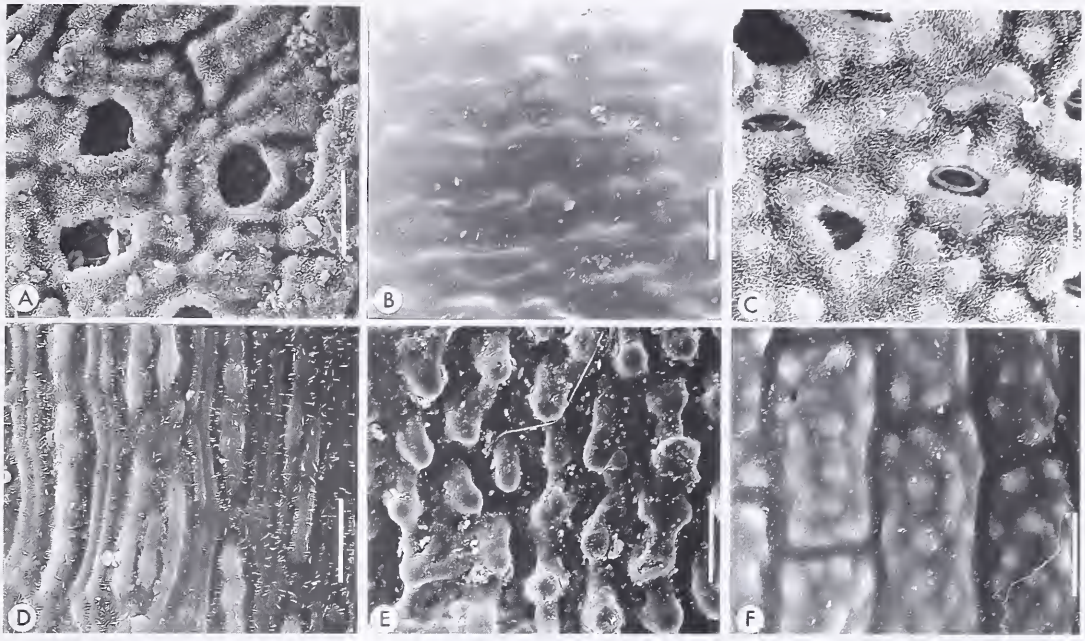

FIGURE 4.—SEM micrographs of cuticular relief in leaves of *Lachnaea* species. A, *L. burchellii, Oliver 9251*, adaxial surface, depressed reticulate-subpapillate; B, *L. grandiflora, Beyers 129*, abaxial surface, subpapillate; C, *L. naviculifolia, Beyers 114*, adaxial surface, papillate; D, *L. nervosa, Oliver 9259*, abaxial surface, reticulate-subpapillate; E, *L. sociorum, Beyers 176*, abaxial surface, striate-papillate; F, *L. striata, Esterhuysen 26861*, abaxial surface, depressed reticulate-subpapillate. Scale bars: A–D, F, 37 µm; E, 92 µm.

the epidermis in *L. aurea* (Beyers & Van der Walt 1995: fig. 8F) and *L. striata*. In *L. macrantha*, however, the mid-bundle is flanked on either side by three lateral bundles, more or less the same size as the mid-bundle, with small intermediate bundles occurring between these two types. Here the extraxylary fibre caps are not well developed abaxially and the uniseriate, parenchymatous bundle sheath is complete.

Crystals of diosmin occurring as sphaerocrystalline to somewhat dendritic masses, pale yellow in colour, may be present either in the epidermis, mesophyll, vascular tissue, extraxylary fibres or in the bundle sheath, or simultaneously in two or more of these tissues (Figure 6 B, C; Beyers & Van Wyk 1998b: fig. 9B). Druse crystals of presumably calcium oxalate (Figures 5A; 6B) are present in most species and may also occur in the mesophyll together with diosmin crystals as in *L. nervosa* (Figure 6B) and *L. ruscifolia*. Visibly stained tanniniferous deposits are usually present except in *L. alpina*, *L. macrantha* and *L. pudens*, and sometimes in *L. nervosa*. These deposits are usually found in the epidermis but in *L. laniflora* (Figure 5A), *L. penicillata* and *L. villosa* they also occur in the parenchymatous bundle sheath. Crystals and tanniniferous deposits have never been observed in the same cell and appear to be mutually exclusive.

Discussion

Anatomical adaptations in the leaves of *Lachnaea* are typical of plants able to withstand the long dry summers of the Mediterranean or semi-Mediterranean climate of the Cape Floristic Region with a rainfall of 200–3 000 mm per annum. Anatomical features in *Lachnaea* correlate with many of those found in selected fynbos species by Van der Merwe *et al.* (1994). Presence of a relatively thick cuticle and epicuticular waxes, and in some species, such as *L. alpina*, the thick periclinal walls of the epidermal cells, are typcal xeromorphic adaptations. A thick cuticle, together with waxes, probably prevents cuticular transpiration and reflects excessive sunlight (Van der Merwe *et al.* 1994). The gelatinized inner periclinal walls of the epidermis with large mucilage content have, according to Bredenkamp & Van Wyk (1999), been erroneously interpreted as a multiseriate epidermis in *Geissoloma* by Carlquist (1990), and in *Struthiola leptantha* Bolus, among other fynbos species, by Van der Merwe *et al.* (1994). Beyers & Van der Walt (1995) also regarded the epidermis with mucilaginous inner walls in *Lachnaea* as a multiseriate epidermis. The mucilaginous inner walls probably represent a water-storing mechanism by fulfilling the function, which in the typical epidermis is assigned to the cell sap (Haberlandt 1914). The mucilage may be involved not only in the water economy of the leaves of xerophytic plants (Lyshede 1977; Fahn 1990) but may also act as a light filter protecting the palisade tissue from excessive radiation (Bredenkamp & Van Wyk 1999). The stomata are sunken in all but four species. In *L. leipoldtii*, *L. penicillata* and *L. villosa*, three of the four species with stomata on the same level as the adjacent epidermal cells, the leaves are adpressed, the branches are tomentose or felted and the leaf margins are densely ciliate. In these taxa the hairs probably

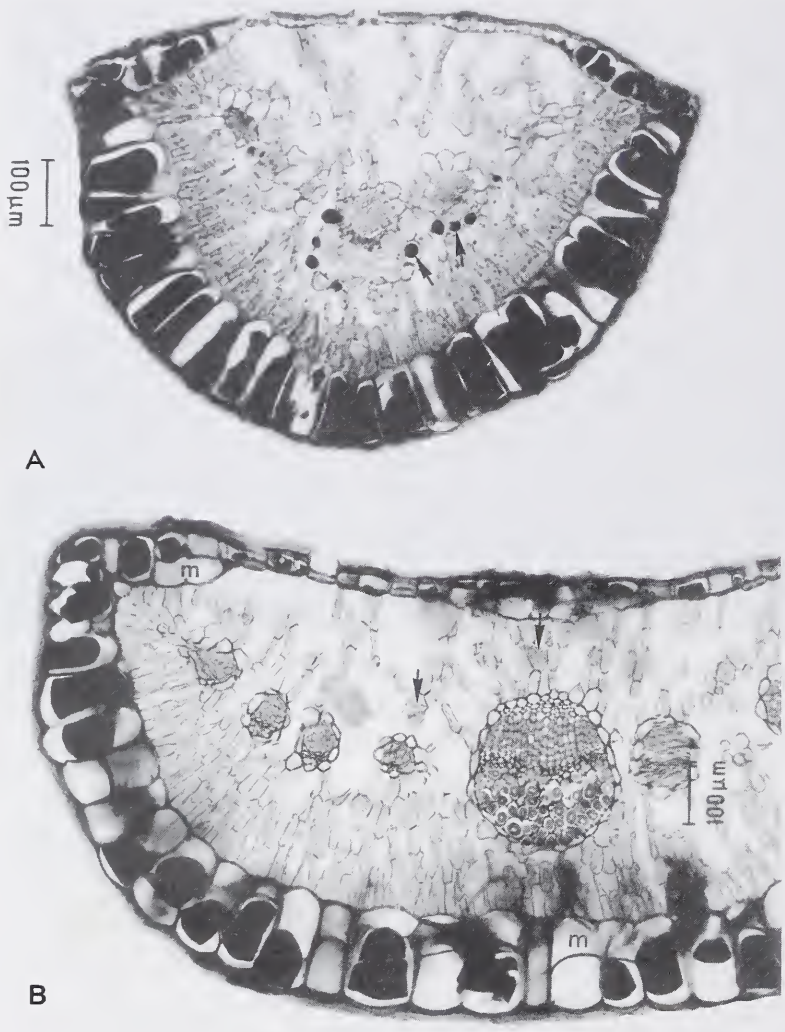

FIGURE 5.—Leaf anatomy in *Lachnaea*: c/s epistomatic, dorsiventral leaves, adaxial face above. A, *L. laniflora, Forsyth 507*, leaf lamina, note tanniniferous epidermal cells (particularly abaxial) and tanniniferous bundle sheath cells (arrowed); B, *L. naviculifolia, Beyers 114*, portion of lamina showing mid and lateral vascular bundles, note gelatinized epidermis (m), tanniniferous epidermal cells, mid-vascular bundle with prominent cap of extraxylary fibres, complete bundle sheath, small lateral vascular bundles with poorly developed extraxylary fibre caps and druse crystals (arrowed) in mesophyll.

decrease air movement over the adaxial epidermis. According to Metcalfe & Chalk (1983) a dense covering of hairs is usually associated with a thin cuticle and with raised rather than sunken stomata, which is an example of an 'anatomical compensation'. In *L. pudens*, the other species with stomata on the same level as the adjacent epidermal cells, the branches are tomentose but the leaves are imbricate, ascending and incurved. The thick adaxial cuticle surrounding the stomata, however, may compensate for the absence of hairs.

An increase of palisade parenchyma at the expense of the development of spongy parenchyma is apparent in *Lachnaea*. Additional palisade is also provided when the leaves become isobilateral. Furthermore, as in the leaves of some xerophytes, the structure of the mesophyll is reversed, with the palisade restricted to the abaxial side in dorsivental leaves (Metcalfe & Chalk 1983). Gibson (1998) found that the typical leaf of nonsucculent desert plants is amphistomatic and the mesophyll is isolateral, with chloroplast-rich palisade cells and little to no spongy mesophyll in the centre. Leaves with such high surface density of palisade cells experience a higher rate of photosynthesis (Gibson 1998).

The prominent extraxylary fibre strands capping the vascular bundles are thought to play a role in protecting the tissues against mechanical injury on desiccation (Esau 1965; Van der Merwe *et al.* 1994). Strands of sclerenchymatic fibres running parallel to the leaf margins in the mesophyll as found in *L. aurea* and *L. striata* were reported by Van der Merwe *et al.* (1994) in *Cliffortia ruscifolia* L., *Passerina glomerata* Thunb., *P. vulgaris* Thoday and *Struthiola leptantha*. These fibre strands seem to offer mechanical support to the leaf margins and protection against tearing (Van der Merwe *et al.* 1994).

Phenolic deposits are present at least in the epidermis of most *Lachnaea* species, but are also present occasionally in the mesophyll and in the bundle sheath cells.

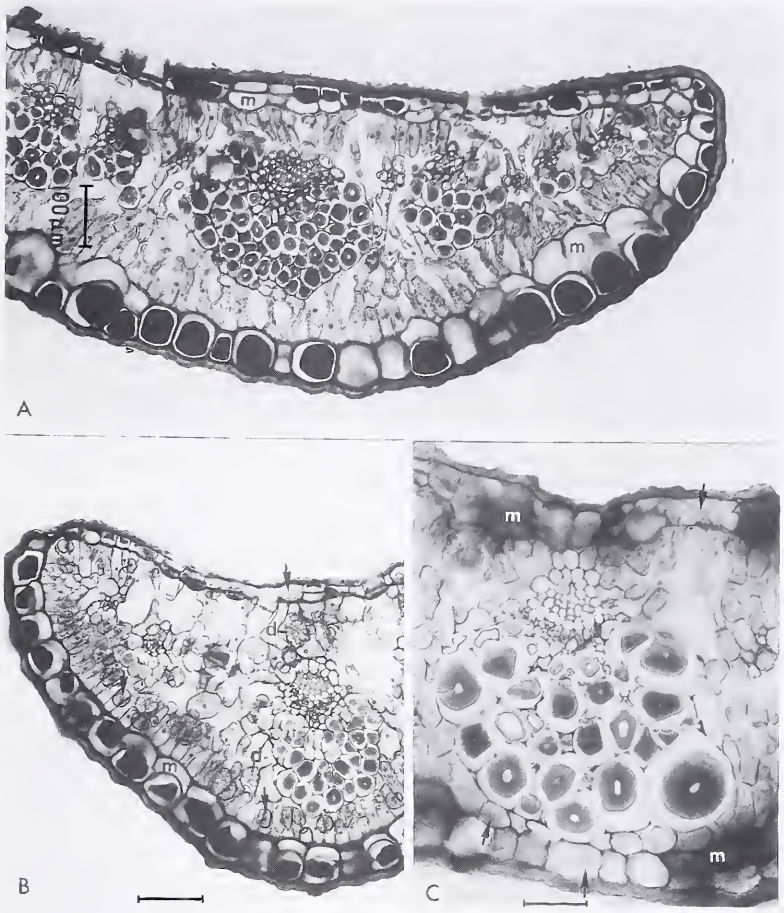

FIGURE 6.—Leaf anatomy in *Lachnaea*: c/s epistomatic, dorsiventral leaves, adaxial face above. A, B, portion of lamina showing mid and lateral vascular bundles: A, *L. glomerata, Beyers 192*, note thick outer wall of adaxial epidermis, gelatinized epidermis (m), tanniniferous epidermal cells, vascular bundles with prominent caps of extraxylary fibres; B, *L. nervosa, Beyers 215*, note diosmin crystals (arrowed) in adaxial epidermis and mesophyll and druse crystals (d) in mesophyll. C, *L. ruscifolia, Vlok 2084*, c/s mid-vascular bundle; note prominent cap of extraxylary fibres extending to abaxial epidermis, masses of diosmin crystals (arrowed) in ad- and abaxial epidermis and mesophyll. Scale bars: B, 100 µm; C, 50 µm.

According to Jordaan & Theunissen (1992), the concentration of tanniniferous substances increases when drought conditions intensify. They are of the opinion that these deposits may be part of an anti-herbivory defence mechanism or that an increase in phenolic substances may also be the result of a disrupted metabolism caused by the high radiation levels of arid regions.

Certain features of two of the four leaf types proposed by Van der Merwe *et al.* (1994), namely the *Myrsine* and *Metalasia* types, can be found in *Lachnaea*. The *Myrsine* type, when dorsiventral, differs from the epistomatic, dorsiventral group of *Lachnaea* by having stomata abaxially and the palisade adaxially. Within *Lachnaea* there is a reduction in leaf width and a gradual change from leaves being more or less flat on both sides to those which are deeply concave adaxially and convex abaxially. Leaves in *L. ericoides* approach the *Metalasia* leaf type, but the adaxial groove is rather wide and lacks unicellular hairs confined to the groove. The leaves of some *Lachnaea* species have in the past been referred to as ericoid (Dyer 1975), but if one defines a leaf with recurved margins forming one or two pockets on its lower side as 'ericoid', then the leaves of *Lachnaea* cannot be considered ericoid.

When the foliage leaves of *Lachnaea* are epistomatic, they are usually either adpressed, ascending or inclined, only occasionally patent or reclined. The divergence from the axis is therefore usually not greater than 75°. The abaxial leaf surface is thus exposed, whereas the adaxial leaf surface is more protected. Additionally the leaves are usually adaxially concave and abaxially convex.

One of the most fundamental of biological problems is the relative influence of heredity and environment on the life form and structure displayed by the various taxa. The usefulness of anatomical characters as indicators of taxonomic affinity should therefore not be judged in isolation (Metcalfe & Chalk 1983). Although acknowledging the fact that leaves respond to ecological factors, the taxonomic value of certain anatomical characters has been found to be very useful within *Lachnaea*, especially the presence of stomata on both surfaces or only adaxially, as well as their position in relation to the adjacent epidermal cells. In *Lachnaea* amphistomatic leaves are found in four species sharing the same inflorescence structure. Two other species, *L. alpina* and *L. macrantha*, both with the same inflorescence structure as the other four species, have epistomatic leaves. *L. macran-*

tha has been included in the group with epistomatic, dorsiventral leaves, but can be regarded as transitional between the two types described above: stomata are only adaxial, the adaxial epidermal cells are slightly smaller than the abaxial ones, and the adaxial palisade-like spongy tissue is similar to the abaxial palisade tissue, differing only in having larger intercellular spaces below the stomata. No phenolic deposits were found in the species with a capitate inflorescence.

Differences in cuticular pattern have been regarded as taxonomically useful at generic or specific level (Cutter 1978; Haron & Moore 1996). The latter authors, however, emphasize that leaf surface features alone are not sufficient for the delimitation of various infrageneric groups and, like all other taxonomic evidence, leaf micromorphological characters should be interpreted with great circumspection.

In *Lachnaea* cuticular relief patterns vary interspecifically and often intraspecifically, for example in *L. nervosa* and *L. gracilis*. It was not always easy to assign a particular descriptive term to a pattern as there tended to be a continuum of variation. Wax deposits, when crusted, may also hide the substructure. According to Cutter (1978) wax patterns vary in different species, and to some extent within a single species under different conditions. Thus, conditions under which plants are grown, including altitude, may affect the form of the wax (Cutter 1978). Cuticular relief in *Lachnaea* was not found to be taxonomically useful at the specific level.

Presence of prominent extraxylary fibre caps associated with the mid- and lateral bundles, as in *L. ruscifolia* and *L. striata*, is expressed externally by the ribbed leaves, and is a useful taxonomic character. Sclerenchymatic fibres running parallel to the leaf margins in the mesophyll in *L. aurea* and *L. striata* are diagnostic for these two species (Table 6).

Mucilaginous epidermal cell walls cannot be used as a taxonomic character at the species level as they are present to varying degrees in all members of the genus. At the family level, however, they have taxonomic relevance, as mucilaginous epidermal cell walls are regarded as a common feature in the Thymelaeaceae (Solereder 1908; Metcalfe & Chalk 1979).

As calcium oxalate crystals are among the most widespread ergastic substances in angiosperms (Metcalfe & Chalk 1983), their taxonomic value at the generic or specific level is not really useful in the Thymelaeaceae. Diosmin crystals have been recorded in certain Lamiaceae and Rutaceae (Metcalfe & Chalk 1983). These crystals occur in eleven *Lachnaea* species and may be of taxonomic relevance within the family. However, no reference has been found to the presence of these crystals in other genera of the Thymelaeaceae.

4.4 INFLORESCENCE MORPHOLOGY

Meisner (1840) established three sections within *Lachnaea* based on the inflorescence morphology: *Sphaeroclinium*, *Conoclinium* and *Microclinium*. In a subsequent publication, he used the same classification (Meisner 1857). He distinguished the following inflorescence types: a terminal, many-flowered capitulum, which is either involucrate or evolucrate (section *Sphaeroclinium*); a terminal or subterminal, few- to many-flowered, evolucrate capitulum (section *Conoclinium*); a terminal, subcapitate or subsolitary inflorescence with sessile flowers (section *Microclinium*); and an axillary, one-flowered inflorescence (section *Microclinium*). Meisner (1840) considered the flowers of *Cryptadenia* to be terminal, solitary or geminate, or occasionally axillary and solitary, but in his publication of 1857 he regarded them as terminal and subsolitary.

Gilg (1894) described the inflorescences of *Lachnaea* as usually terminal, many-flowered heads, but occasionally, when consisting of two flowers, as mostly axillary. He regarded the flowers of *Cryptadenia* as solitary and axillary with two bracteoles.

Domke (1934) considered the inflorescences to be usually terminal, involucrate capitula or congested capitula without an involucre. In his generic description no mention was made of the solitary-flowered inflorescences. In *Cryptadenia* he regarded the flowers as solitary or few, either terminal or axillary with two bracteoles.

According to Dyer (1975) the inflorescences in *Lachnaea* are either terminal, bracteate or ebracteate heads or congested spikes, or rarely one-flowered, whereas in *Cryptadenia* the flowers are solitary and terminal or axillary.

Weberling & Herkommer (1989) considered the inflorescences of *Lachnaea* to be capitate or spicate, or as consisting of solitary, axillary flowers borne on a proliferating spike. In *Cryptadenia* they regarded the flowers as being solitary and terminal. They described the terminal, single-flowered inflorescence found in *Cryptadenia* as a monotelic inflorescence and the ramification type of the polytelic synflorescences of the Thymelaeaceae as thyrsic. These synflorescences have, according to them, been reduced to racemes, spikes or umbels in certain genera, and in others, such as *Lachnaea*, the umbel-like aggregation of flowers is combined with the formation of an involucrum.

Beyers & Van der Walt (1994) investigated the inflorescence morphology of 14 species of *Lachnaea* and four species of *Cryptadenia*. They concluded that the flowers in *Lachnaea* are arranged in terminal, indeterminate, capitate or umbellate inflorescences, or that they are solitary and terminal. The capitula are multiflowered and ebracteate and are borne singly at the end of branches on sericeous peduncles. The indeterminate umbels are sessile and either ebracteate as in *L. burchellii*, *L ericoides* and *L. nervosa* or bracteate as in *L. eriocephala*. In both *L. axillaris* and *L. ruscifolia*, Beyers & Van der Walt (1994) found the solitary flowers to be terminal, contrary to the opinion of previous authors. They also considered the flowers in *Cryptadenia* to be solitary and terminal.

Observations

The inflorescence morphology as interpreted by Beyers & Van der Walt (1994) is followed here although some aspects need comments. Inflorescence characters are summarized in Table 8. The diameter of the inflorescences is measured from the extremities of the outermost flowers. In capitula and umbels, flower development is sequential. The fruiting stage may be present while buds are still developing in the inner parts of the inflorescence. The number of flowers in an inflorescence is therefore not easily determined. Once all the flowers are shed, the floral scars remaining on the floral axis of the capitate inflorescences, or on the pedicels of the umbellate inflorescences, which remain for some time, are counted; in this way a more accurate count can be achieved. For comparative purposes, however, the highest number of mature flowers at a given time, is given here.

Both indeterminate and determinate inflorescences occur in *Lachnaea*.

TABLE 8.—Inflorescence characters of *Lachnaea*

Species	Determinate inflorescences with solitary flower	Indeterminate inflorescences							
		Capitulum	Umbellate						
			Ebracteate	Pseudobracteate	Bracteate	Diam. mm	No. mature flowers at any one time	No. involucral bracts	No. bract-like leaves
axillaris	×								
filicaulis	×								
gracilis	×								
grandiflora	×								
laxa	×								
leipoldtii	×								
pudens	×								
pusilla	×								
ruscifolia	×								
uniflora	×								
alpina		×				15–25	up to 40		
capitata		×				5–16	up to 8		
densiflora		×				8–16	up to 22		
filamentosa		×				30–100	>100		
macrantha		×				35–60	> 50		
pomposa		×				25–55	> 50		
diosmoides			×			3–15	up to 20		
ericoides			×			3–8	up to 4		
sociorum			×			8–15	up to 9		
stokoei			×			4–6	up to 3		
striata			×			8–20	up to 12		
burchellii			×			4–10	up to 10		
glomerata			×			5–10	up to 8		
nervosa			×			6–15	up to 5		
elsieae				×		to 2	up to 4		4
eriocephala				×		25–55	up to 30		2–4
greytonensis				×		5–7	up to 5		4
laniflora				×		8–15	up to 14		4
marlothii				×		5–10	up to 4		4
naviculifolia				×		18–35	up to 15		4–6
rupestris				×		5–7	up to 5		4
villosa				×		2–4	up to 3–5*		4
aurea					×	20–55	up to 30	6–8	
funicaulis					×	4–8	up to 6	4	
globulifera					×	5–20–25*	up to 16	2	2
montana					×	10–30	up to 20	2	2
oliverorum					×	8–15	up to 6	4	
pedicellata					×	7–15	up to 8	2	2
pendula					×	3–5	up to 8	4	
penicillata					×	3–4	1	4	

* occasional occurrence.

FIGURE 7.—Inflorescences of *Lachnaea* species. A, G, J, bracteate umbels: A, *L. aurea, Oliver 10550* (life size); G, *L. pedicellata, Beyers 260*; J, *L. funicaulis, Bolus 5316*. B–D, ebracteate umbel: B, *L. burchellii, Oliver 9251*, note bracteose leaves (arrowed) subtending flowers; C, *L. diosmoides, Beyers 181*; D, *L. nervosa, Oliver 9258*, note sharp differentiation between lower foliage leaves and those subtending inflorescence and lateral shoot (arrowed); E, F, ebracteate capitulum: E, *L. capitata, Beyers 138*, note peduncle (arrowed); F, *L. filamentosa, Beyers 110* (life size), note convex floral axis and vegetative bud (arrowed) in axil of distal leaf. H, terminal, one-flowered inflorescence: *L. filicaulis, McDonald 1989*, note lateral shoot (arrowed) in axil of distal leaves; I, *L. greytonensis, Beyers 209*, pseudobracteate umbel, note superficial similarity of inflorescences between I and J. b, involucral bract; bl, bract-like leaf.

Indeterminate inflorescences

Within the indeterminate inflorescences both the capitulum and the umbel are represented.

Capitulum (Figure 7E, F; Tables 8; 9)

Six species have terminal, multiflowered, ebracteate capitula. The diameter of the inflorescences varies from 5–100 mm. These capitula are borne singly at the end of the branches on peduncles, which vary in length from 1–20 mm. The indumentum of the peduncles varies from densely hairy to puberulent only near the apex. The sessile flowers are arranged on a moderately thick, convex floral axis, which elongates during the flowering period. In *L. filamentosa* more than a hundred mature flowers may be present, whereas in *L. capitata* not more than eight have been seen (Table 9).

Umbel

Beyers & Van der Walt (1994) distinguish only between ebracteate and bracteate umbels, but a further, intermediate type is here proposed. Three groups are therefore recognized: (a) ebracteate, (b) pseudobracteate and (c) bracteate umbels.

(a) Ebracteate umbel (Figure 7B–D; Table 8)

Eight species have ebracteate umbels which vary between 3–20 mm in diameter, with up to 3–20 mature flowers at a given time. These umbels are subtended by

TABLE 9.—Diagnostic characters in *Lachnaea* species with a capitate inflorescence

Species	Size diam. mm	No. mature flowers at any one time	Peduncle		Receptacle		
			length mm	indumentum	shape	size mm	indumentum
alpina	15–25	up to 40	3.0–20.0	sericeous-hirsute	subconical	2.0–3.2 × 2.2–3.5	sericeous
capitata	5–16	up to 8	3.0–6.0	sericeous	hemispherical to cylindrical-conical	0.9–20.2 × 1.5–6.0	sericeous
densiflora	8–16	up to 22	5.0–10.0	sericeous or tomentose-sericeous	hemispherical to conical to widely conical	2.0–8.0 × 3.4–7.5	sericeous
filamentosa	30–100	up to >100	1.0–15.0	sericeous	narrowly conical to conical	5.0–25.0 × 2.0–11.0	puberulent
macrantha	35–60	up to >50	2.0–3.0	puberulent near apex	oblong conical to ellipsoid	4.0–5.5 × 1.8–2.2	puberulent
pomposa	25–55	up to >50	1.0–10.0	sericeous-hirsute	subconical–conical	4.0–12.0 × 2.8–6.0	puberulent

foliage leaves which do not usually differ from the leaves on the rest of the branches. In *L. nervosa* (Figure 7D) however, the inflorescences may be subtended by leaves differing from the rest of the leaves. A sharp differentiation between the lower foliage leaves and the 4–8 distal ones close to the inflorescence was observed: the distal leaves are closely set and the lower ones among them are noticeably shorter than the foliage leaves below them. These foliage leaves gradually become broader and longer, but are still up to three times narrower than the 4–8 distal ones above them. Differentiation of the distal leaves may also occur in *L. burchellii* (Figure 7B) and *L. conglomerata*. In both species these leaves differ in size and shape from the foliage leaves on the rest of the plant. This is particularly noticeable on the short, lateral flowering branches. Differentiation of the leaves on the main flowering branches may possibly be ascribed to unfavourable ecological conditions which cause the terminal growth to undergo a dormancy period. Under favourable conditions growth is stimulated and a relatively short shoot with a terminal inflorescence develops.

(b) Pseudobracteate umbel (Figure 7I; Table 10)

Eight species have pseudobracteate umbels. These umbels resemble capitula and are 2–55 mm in diameter, with up to 3–30 mature flowers at a given time. The distal 2–6 leaves are closely set and partially enclose the inflorescence. They differ in shape, size and often texture and indumentum from the rest of the foliage leaves. These subtending leaves are bract-like and similar to the involucral bracts of the bracteate umbel. Although the inflorescences appear to be similar to the bracteate umbels, they differ from the latter by the development of new vegetative growth in the axils of the bract-like leaves. These bract-like leaves also differ from those found in the ebracteate umbels in *L. nervosa*, *L. burchellii* and *L. glomerata* where the lower leaves of the distal group of leaves are noticeably shorter than the foliage leaves below. In the pseudobracteate umbels there is no sharp transition between the foliage leaves and those subtending the inflorescence. Here a dormancy period is not inferred.

New growth in the axils of the bract-like leaves is not always easily detected, especially on herbarium sheets, and careful scrutiny is required. The inflorescence of *L. eriocephala*, which in previous publications (Weberling & Herkommer 1989; Beyers & Van der Walt 1994) has been regarded as involucrate, actually belongs to the pseudobracteate type since vegetative shoots were observed in the axils of the distal 'bracts' [voucher: *Beyers 238* (NBG)].

(c) Bracteate umbel (Figure 7A, G, J; Table 11)

Eight species have bracteate umbels. These umbels resemble capitula and are 3–55 mm in diameter, with 1–30 mature flowers at a given time. The flowers are partially enclosed by 2–8 closely set bracts. With the exception of *L. aurea* (Figure 7A), which has 6–8 bracts, the species in this group appear to have four bracts. On closer examination it was found that in three species, only the distal pair of bracts were true bracts and that in the axils of the subdistal pair, vegetative growth occurred, as in *L. pedicellata* (Figure 7G). These bracts are therefore bract-like leaves, similar to those found in the pseudobracteate umbels. The bracts and bract-like leaves differ in shape, size and often texture as well as indumentum from the normal foliage leaves.

Determinate inflorescences (Figure 7H; Table 8)

In ten species of *Lachnaea* the flowers are solitary and terminal. In some species, for example *L. axillaris* and *L. ruscifolia*, reduced lateral branches, each terminated by a solitary flower, develop at random on the

TABLE 10.—Diagnostic characters of pseudobracteate umbel in *Lachnaea*

Species	Diam. mm	No. mature flowers	No. bract-like leaves	Shape	Size	Abaxial surface	Margin	Apex
elsieae	1.5–2	up to 4	4	narrowly elliptic to obovate	1.6–4.0 × 0.9–2.0	glabrous	membranous to brown scarious, ciliate	subacute to obtuse or emarginate
eriocephala	25–55	up to 30	2–4	elliptic to widely obovate to oblate	5.2–17.0 × 3.6–14.0	glabrous or sparsely adpressed hairy	membranous, ciliate	acuminate to mucronate
greytonensis	5–7	up to 5	4	obovate	2.9–4.2 × 1.6–2.3	glabrous	villous-ciliate	acute to obtuse
laniflora	8–15	up to 14	4	elliptic to widely elliptic to obovate	2.9–5.1 × 2.1–3.0	glabrous	glabrous to ciliolate*	subacute
marlothii	5–10	up to 4	4	elliptic to obovate	2.9–4.1 × 1.2–2.7	glabrous	villous-ciliate	acute to obtuse
naviculifolia	18–35	up to 15	4–6	elliptic to very widely elliptic or obovate to very widely obovate	6–21 × 4–13	glabrous or adpressed hairy at apex	membranous (upper $^1/_2$) ciliolate	cuspidate to mucronate
rupestris	5–7	up to 5	4	elliptic to widely elliptic or obovate to widely obovate	3.2–5.0 × 1.6–2.9	glabrous	ciliate	mucronulate, acute to cuspidate
villosa	2–4	up to 3–5*	4	elliptic to widely elliptic or obovate	2.3–3.2 × 1.1–2.2	glabrous	brown lanate-ciliate	rounded to obtuse

* occasional occurrence.

main flowering branches within the same flowering period. Consequently the main flowering branch may have the appearance of a racemose or spicate inflorescence. In other species the main flowering branches are terminated by the solitary flower, and the new proliferating shoots, which develop in the axils of the distal leaf pair immediately behind the flower, may be terminated by a solitary flower either in the same or only in the following flowering period.

Discussion

Inflorescence morphology is of considerable taxonomic importance in *Lachnaea*. On the basis of the inflorescence morphology three main inflorescence types can be distinguished, namely, 1, the determinate, solitary-flowered inflorescence; 2, the indeterminate capitulum; and 3, the indeterminate umbel. Within the umbellate inflorescence three groups, namely ebracteate, pseudobracteate and bracteate umbels are recognized. In the latter two groups the shape, texture and indumentum of the bracts or bract-like leaves have taxonomic relevance.

Following Weberling & Herkommer (1989) the terminal, solitary-flowered inflorescence in *Lachnaea* can be regarded as monotelic, and the capitulum and umbel as polytelic. Weberling (1983) postulated that the polytelic type of inflorescence has probably been derived repeatedly from the monotelic type during the evolution of angiosperms by the reduction of the terminal flower and specialization of the paracladia of the monotelic system. Thus the floral axis, instead of terminating in a single flower, terminates in a multiflowered polytelic inflorescence.

Within the Thymelaeaceae, Weberling & Herkommer (1989) found that *Gonostylus* Teijsm. & Binn. and *Amyxa* Tiegh. of the Gonostyloideae, which is regarded as a relatively primitive group, have monotelic inflorescences. Within the Thymelaeoideae they also found that certain taxa have monotelic inflorescences. They concluded that 'regarding the various combinations of the other, more or less primitive characters and the different taxonomical evaluation of these combinations, it appears to be impossible to draw any taxonomic conclusions exclusively from the existence of the monotelic inflorescence within these taxa'.

In postulating the evolutionary development of the multiflowered inflorescence structure within *Lachnaea,* one could argue that two pathways were followed from an hypothetical racemose inflorescence, namely, 1, to the capitulum with the thickened floral axis; and 2, to

TABLE 11.—Diagnostic characters of bracreate umbel in *Lachnaea*

Species	Diam. mm	No. mature flowers at any one time	No. involucral bracts	Shape	Size	Abaxial surface	Margin	Apex	No. bract-like leaves	Shape	Size	Abaxial surface	Margin	Apex
aurea	20–55	up to 30	6–8	narrowly elliptic to elliptic or obovate	11.5–19 × 4.5–11	glabrous or sericeous in middle	membranous, yellow	mucronulate to acuminate						
funicaulis	4–8	up to 6	4	narrowly obovate to ovate	3.5–4.6 × 1.8–2.5	glabrous	tinged brown, lanate-ciliate	obtuse or truncate to sub-emarginate						
globulifera	5–15(25*)	up to 16	2	ovate or widely elliptic to widely obovate	4.5–6.0(10.0*) × 2.3–4.5(7.0*)	glabrous	membranous, ciliate	acute, mucronate or acuminate	2	narrowly elliptic to widely elliptic, ovate to obovate	3.5–6.8(10*) × 1.7–3.5(6*)	glabrous or adpressed pilose near margin	membranous, ciliate	acute to acuminate
montana	10–30	up to 20	2	elliptic to widely ovate or obovate	7.5–12.0 × 4.0–6.0	glabrescent to tomentose	membranous (upper $^1/_2$); yellow	mucronulate or cuspidate	2	elliptic to obovate	6.5–12.0 × 3.5–8.5	glabrescent to tomentose	membranous (upper $^1/_2$); yellow	mucronate to cuspidate
oliverorum	8–15	up to 6	4	ovate to obovate	4.7–7.0 × 2.3–3.7	glabrous	lanate-ciliate	acute to rounded						
pedicellata	7–15	up to 8	2	elliptic to obovate to widely obovate	6.0–7.5 × 3.0–7.0	glabrous	membranous (upper $^1/_2$); yellow	mucronulate or shortly cuspidate	2	obovate to widely obovate	5.5–7.2 × 3.2–5.0	glabrous	membranous (upper $^1/_2$); yellow	apiculate to cuspidate
pendula	3–5	up to 8	4	clliptic to obovate to widely obovate	2.0–2.5 × 1.2–2.2	glabrous	tinged brown, white-ciliate	rounded to obtuse						
penicillata	3–4	1	4	narrowly elliptic to obovate	3.0–4.0 × 1.0–2.0	glabrous	scarious, brown; upper $^1/_2$ ciliate, lower $^1/_2$ lanate-ciliate	rounded to emarginate						

* occasional occurrence.

FIGURE 8.—Diagrams of hypanthia illustrating position of circumscissile articulation (....) and different shapes of upper portion of hypanthium in *Lachnaea*. A–L, upper portion not narrowing into a tube at base (not stalked): A, *L. grandiflora*; B, *L. uniflora*; C, *L. stokoei*; D, *L. filicaulis*; E, *L. gracilis*; F, *L. capitata*; G, *L. aurea*; H, *L. pudens*; I, *L. leipoldtii*; J, *L. pusilla*; K, *L. gracilis*; L, *L. axillaris*. I–L, upper portion with basal invagination; M–Gg, upper portion narrowing into a tube at base (stalked) although tube may be very short. M–S, U, V, X, Y, Ee–Gg, upper portion funnel-shaped: M, *L. densiflora*; N, *L. funicaulis*; O, *L. ericoides*; P, *L. ruscifolia*; Q, *L. diosmoides*; R, *L. striata*; S, *L. alpina*; U, *L. burchellii*; V, *L. villosa*; X, *L. penicillata*; Y, *L. nervosa*; Ee, *L. globulifera*; Ff, *L. glomerata*; Gg, *L. marlothii*. T, W, upper portion cup-shaped narrowing into a tube at base: T, *L. greytonensis*; W, *L. oliverorum*. Z–Dd, upper portion narrowly funnel-shaped: Z, *L. pomposa*; Aa, *L. montana*; Bb, *L. macrantha*; Cc, *L. filamentosa*; Dd, *L. eriocephala*.

the sessile flowers and the umbel, through the shortening of the floral axis. The umbellate infloreseenee evolved further from the ebraeteate through the pseudobraeteate to the bracteate state.

Classen-Boekhoff (1990) found that pseudanthia oeeur in more than 40 angiosperm families. The eephalium is the type of indeterminate inflorescence from whieh pseudanthia have most frequently developed

(Classen-Bockhoff 1990). Within the Thymelaeaceae she reported hyperfloral pseudanthia in *Pimelea* Banks & Sol. ex Gaertner. Similar pseudanthia occur in many *Lachnaea* species. Here are included those species which have either pseudobracteate or bracteate umbels. One could also interpret the capitate inflorescences in *Lachnaea* as pseudanthia. In *L. macrantha*, with strongly zygomorphic flowers, the inflorescence appears daisy-like. Here the pseudanthia are composed exclusively of flowers.

4.5 FLOWER MORPHOLOGY

Within the Magnoliophyta, flowers have traditionally been regarded as conservative organs and of great taxonomic importance. A literature survey of the Thymelaeaceae reveals the confusion which exists with regard to the identity of the petaloid structures and the floral tube and whether the ovary of the unilocular Thymelaeoideae is composed of one or two carpels. Naturally the interpretation of the above has a direct bearing on the taxonomic position of the family.

Earlier classifications of the Thymelaeaceae, including that by Domke (1934), have to a large extent been dependent on the floral morphology.

In the past treatments of *Lachnaea* (Meisner 1840, 1857; Baillon 1880; Gilg 1894; Wright 1915; Domke 1934; Dyer 1975) and *Cryptadenia* (Meisner 1840, 1857; Gilg 1894; Wright 1915; Domke 1934; Dyer 1975) the floral morphology was considered to be of great taxonomic importance. The position of the floral scales deep down in the hypanthium was one of the major considerations by Meisner (1840) for establishing the genus *Cryptadenia*. In the generic delimitation of *Lachnaea* and *Cryptadenia* Beyers & Van der Walt (1995) dealt with the floral morphology in detail.

Pedicel

Flowers in *Lachnaea* are either sessile or pedicellate. A ring of trichomes occurs at the basal articulation of the sessile flowers of the solitary-flowered species. In the pedicellate flowers the pedicels are variable in length, shape and indumentum. They may be terete as in *L. diosmoides* or dorsiventrally flattened as in *L. naviculifolia*. The flowers may be terminally attached to the pedicels or the pedicels may be abaxially elongated beyond the insertion of the flower as in the latter species. In all the species with ebracteate umbels as well as in *L. aurea* and *L. laniflora*, the pedicels hardly elongate in the fruiting stage, whereas in the other species they may elongate considerably in the fruiting stage and remain within the inflorescence long after the fruits have been shed, as in *L. eriocephala*.

Hypanthium

Saunders (1939), Heinig (1951), Heads (1990) and Beyers & Van der Walt (1995) regard the floral tube in Thymelaeaceae as a hypanthium. The hypanthium in the Thymelaeaceae has been interpreted as being appendicular (foliar) by Meisner (1857), Wright (1915), Saunders (1939), Heinig (1951), Peterson (1959), Dyer (1975), Beyers & Van der Walt (1995) and Bredenkamp & Beyers (2000), or as being receptacular by Eichler (1878), Baillon (1880), Gilg (1894), Wettstein (1935), Rendle (1938) and Bunninger (1972).

The floral tube is a hypanthium and interpreted as being appendicular in origin (Beyers & Van der Walt 1995). A circumscissile articulation is always present, as in several other Thymelaeaceae, e.g. *Drapetes* Banks ex Lamarck (Heads 1990), *Gnidia* (Peterson 1959) and *Struthiola* (Bredenkamp & Beyers 2000). The position of the articulation expressed as a fraction of the length of the basal portion to the total length varies from one-fifth to four-fifths. The upper portion of the hypanthium abscises soon after seedset. The length of the hypanthium varies from 1.2–20.0 mm. In some species the variation in length can be considerable, as in *L. eriocephala*, *L. filamentosa* and *L. grandiflora*.

The portion of the hypanthium above the circumscissile articulation is hereafter referred to as the upper portion, and below the articulation as the basal portion.

The shape of the upper portion of the hypanthium varies from narrowly funnel-shaped to funnel-shaped or cup-shaped narrowing into a tube at the base, or widely cup-shaped to cup-shaped with or without a basal invagination, or narrowly obconical to widely obconical with or without a basal invagination (Figure 8). The indumentum inside and outside is variable but all the trichomes, when present, are acicular.

The shape of the basal portion of the hypanthium varies from narrowly ellipsoid to ellipsoid, narrowly ovoid to broadly ovoid, narrowly obovoid to widely obovoid, or may be oblong or pyriform. The shape may be constant or vary within a species. In *L. gracilis*, for example, the shape of the basal portion of the hypanthium may vary from narrowly ellipsoid to ellipsoid or from narrowly ovoid to ovoid, in *L. naviculifolia* from ellipsoid to obovoid and in *L. grandiflora* from narrowly ellipsoid to ellipsoid or occasionally widely obovoid. The basal portion of the hypanthium is, in all but five species, glabrous within. On the outside the basal portion can be glabrous or variously pubescent. The trichomes, when present, are usually acicular but in *L. burchellii*, *L. nervosa*, *L. pusilla* and *L. uniflora* they are subacute to obtuse, thus differing from the acicular trichomes on the outside of the upper portion of the hypanthium.

Calyx

The calyx consists of four sepals arising on the rim of the hypanthium. The petaloid calyx is white, cream, cream with a pink to mauve or blue tinge, varying shades of pink, blue or mauve, or occasionally yellow or dark red. The sepals vary in shape and size from almost equal to distinctly unequal, but with a gradual transition from one state to the other. In the distinctly zygomor-

phic forms the anterior sepal is usually the longest and the posterior one the shortest, as in *L. filamentosa*. In *L. macrantha*, however, the lateral sepals and the posterior sepal are much reduced, with the anterior sepal being three to four times longer than the other three. The shape and size of the sepals vary inter- and infra-specifically. The smallest sepals occur, among others, in *L. greytonensis* (0.8–1.3 mm long), *L. pendula* (0.9–1.7 mm long) and *L. stokoei* (1.1–1.8 mm long), whereas the largest sepals are the anterior ones in *L. macrantha* and *L. filamentosa*, which may attain a length of 16.3 mm and 30 mm respectively. The abaxial surfaces of the sepals are in all but one species, *L. axillaris*, pubescent. The indumentum is either sericeous, sericeous-tomentose, tomentose or villous-tomentose abaxially. The adaxial surface may be glabrous, glabrescent or variously pubescent, but usually the density of the indumentum is less than that of the abaxial surface. The aestivation of the sepals is decussate-imbricate.

Androecium

Eight stamens in two whorls of four are present in all taxa. In some species, as in *L. aurea*, *L. laxa* and *L. villosa*, however, the two whorls are very close to each other, and have the appearance of a single whorl. In the outer stamen whorl, the antesepalous stamens are episepalous or inserted on the hypanthium. When episepalous they may arise at the base of the sepals, close to the rim of the hypanthium, or up to a third way up the sepals. When inserted on the hypanthium their position may vary from arising on the rim to a third way down the upper portion of the hypanthium. The inner stamen whorl, the antepetalous stamens, arise on or very close to the rim to two-thirds way down the upper portion of the hypanthium. Filaments of the antesepalous stamens are usually longer than those of the antepetalous ones, although in some species they may be of equal length, as in *L. alpina*. Occasionally the antesepalous stamens, which arise on the anterior sepal, as in *L. filamentosa*, may be shorter than those of the antepetalous stamens. Conspicuous ridges formed by the adnation of the filaments to the inner wall of the upper portion of the hypanthium are present in some species, e.g. in *L. gracilis*, *L. grandiflora* and *L. pudens*. The anthers are basifixed and introrse, the shape varying from oblong to ellipsoid to spheroid to depressed spheroid. The length of the anthers varies from 0.2–2.6 mm. Anthers with broad connective tissue are present in seven species. In all the species the antesepalous stamens are exserted, and in most species the antepetalous ones are also exserted. In nine species, however, the anthers of the antepetalous stamens are either fully or partially exserted or enclosed.

Floral scales

In the different genera of the Thymelaeaceae organs comparable to the scales in *Lachnaea* have been interpreted by various authors as petals which are reduced or greatly modified in form (Eichler 1878; Gilg 1894; Domke 1934, Wettstein 1935; Rendle 1938; Hutchinson 1959), as aborted stamens (Endlicher 1836–1840), as petaloid glands (Payer 1857 in Heinig 1951), as scales (Meisner 1857; Baillon 1880; Bentham & Hooker 1880; Heads 1990; Beyers & Van der Walt 1995), as mere outgrowths of the perigynium (Velenovský in Heinig 1951), as squamellae which should be regarded either as new structures of uncertain origin or modified parts of the androecium (Moore 1919 in Heinig 1951), or as stipules (Heinig 1951). A brief account of these various interpretations by different authors (from their generic descriptions of *Lachnaea* and *Cryptadenia*) is presented in Table 12.

Floral scales arising on the floral tube also occur in various other families. In the monogeneric Oliniaceae, Rao & Dahlgren (1969) concluded that the floral scales inserted above the stamens and alternating with the petals are most probably stipular appendages of the sepals, since there is evidence of rudimentary stipules in the leaves of *Olinia* Thunb. In the Apocynaceae (including Periplocaceae and Asclepiadaceae) the corolline coronas were considered homologous with colleters in the axil of vegetative leaves and sepals by reason of positional correspondence and ontogenetic similarity (Kunze 1990).

TABLE 12.—Interpretation of hypanthium, petals, scales and gynoecium of *Lachnaea* by various authors

Author	hypanthium (floral tube)	petals	scales	gynoecium
Meisner 1840	appendicular	absent	scales	uniloculate
Meisner 1857	appendicular	absent	scales	uniloculate
Baillon 1880	receptacular	absent	scales	uniloculate
Bentham & Hooker 1880	appendicular	absent	scales	uniloculate
Gilg 1894	receptacular	absent	receptacular outgrowths	uniloculate
Wright 1915	appendicular	absent	scales	uniloculate
Domke 1934	appendicular	present	petaloid scales	uniloculate
Saunders 1939	appendicular	absent	not specified	pseudomonomerous
Heinig 1951	appendicular	absent	stipular appendages of the sepals	pseudomonomerous
Dyer 1975	appendicular	absent	scales	uniloculate
Beyers & Van der Walt 1995	appendicular	absent	scales	pseudomonomerous

TABLE 13.—Floral scales of selected species of *Lachnaea* studied with scanning electron microscope (SEM) and tested with neutral red to ascertain whether they are nectariferous (osmophores). All voucher specimens housed at NBG

Species	Voucher specimens	SEM	Tested with neutral red		Fluid on scales	Fluid at base of scales
			positive	negative		
aurea	*Oliver 10550*	×	×			×
capitata	*Beyers 138*	×				
	Oliver 10519			×		×
densiflora	*Beyers 244*			×		×
eriocephala	*Beyers 237*			×		×
	Beyers 238			×		×
	Rugge s.n.	×	×			×
filamentosa	*Beyers 110*	×				
	Beyers 245		×			×
	Hansford 47			×		×
globulifera						
subsp. *globulifera*	*Beyers 240*		×			×
subsp. *incana*	*Beyers 246*		×			×
gracilis	*Oliver 10415*	×		×	×	
grandiflora	*Beyers 129*	×				
	Beyers 241			×	×	
	Beyers 248		×		×	
	Beyers 250			×	×	
laniflora	*Oliver 10679*		×			×
montana	*Beyers 267*	×				
naviculifolia	*Hansford, M. s.n.*		×			×
oliverorum	*Oliver 10478*	×		×	×	
pedicellata	*Beyers 260*		×			×
pomposa	*Beyers 122*		×			×
pusilla	*Beyers 243*			×	×	
uniflora	*Beyers 136*	×				
villosa	*Beyers 125*	×				
	Du Toit s.n.		×			×

Eight scales arise on the inside of the upper portion of the hypanthium below the point of origin of the antepetalous stamens and alternating with the stamens. The position of the scales varies within the species from arising just below the rim of the hypanthium to just above the circumscissile articulation. They are either exserted or enclosed, and in most species they are basally attached. They are usually terete, but may vary from linear, narrowly oblong, capitate, narrowly obovoid to obovoid, or narrowly ovoid to ovoid or subspheroid. However, in *L. ruscifolia* the scales are laterally flattened. In *L. filicaulis* they are basally and partly abaxially attached to the hypanthium. In three species, *L. grandiflora*, *L. stokoei* and *L. uniflora* they are semiterete, and abaxially attached to the inner wall of the hypanthium. The shape of these scales varies from oblong, narrowly elliptic to elliptic or circular in outline. They are either translucent white, white or yellow and usually glabrous. In *L. alpina*, *L. burchellii*, *L. filamentosa* and *L. pomposa* they are pubescent.

The scales of 15 species were treated with neutral red solution to ascertain whether they are nectariferous or functioning as osmophores (Table 13). Some species tested positive, whereas in some species of which more than one specimen was tested, both positive and negative results were obtained. Other species tested negative although tiny droplets of fluid were observed on the scales, as in *L. gracilis* and *L. oliverorum*. In some species moisture was observed at the base of the scales. Unfortunately the amount of liquid collected from these flowers was miniscule and tests for sugars could not be carried out. SEM micrographs taken of the scales of selected species showed that no stomata are present (Figure 9).

According to Beyers & Van der Walt (1995) anatomical evidence obtained from transections of flowers from a number of species showed that no vascular tissue is present in or at the base of the scales, even when they arise in close juxtaposition to the sepal lateral bundles and the sepal midrib bundles where a rich vascular plexus is present. They found that in some species, as in *L. capitata*, the scales appeared to be non-glandular. In other species as in *L. axillaris*, the scales appeared to be glandular since they are composed of compact thin-walled cells rich in cytoplasm with large nuclei. According to Heads (1990) the gland scales in *Kelleria* (Thymelaeoideae), when fully developed, are turgid, bright yellow and secrete liquid. In other flowers the glands are small, white, and non-secretory (Heads 1990). In *L. gracilis* the scales are translucent white or yellow and in *L. oliverorum* they are translucent white, yet droplets of fluid were observed on them. The colour of the scales in *Lachnaea*, therefore, does not indicate whether they are nectariferous or not.

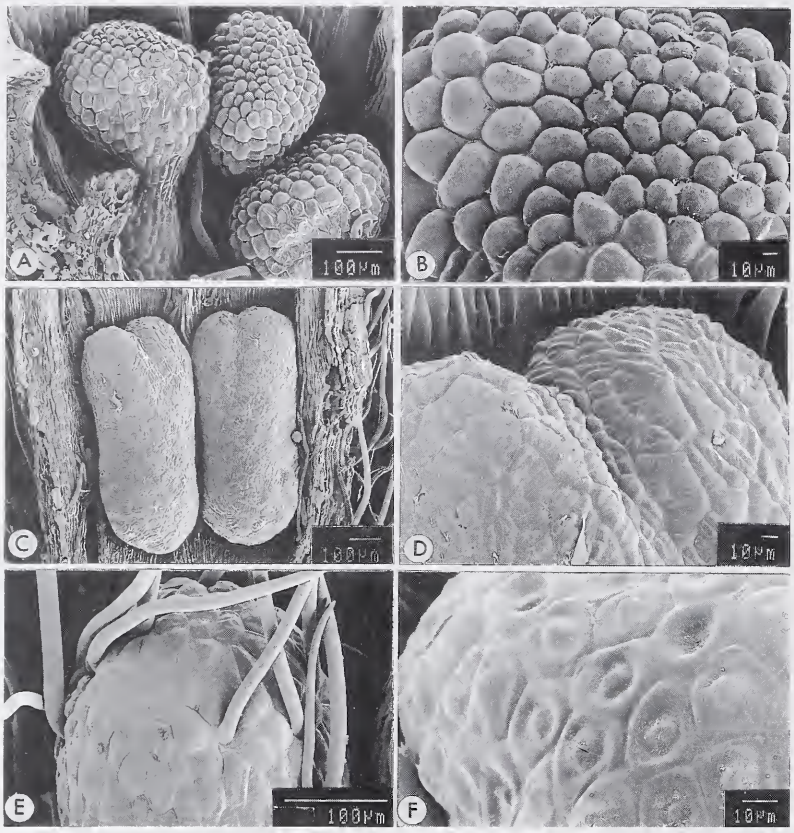

FIGURE 9.—SEM micrographs of floral scales of *Lachnaea* species. A, B, *L. oliverorum, Oliver 10478*: A, capitate scales attached basally to inner wall of hypanthium; B, apical portion of scale. C, D, *L. uniflora, Beyers 136*: C, scales abaxially attached to inner wall of hypanthium; D, apical portion of scale. E, F, apical portion of scales: E, *L.filamentosa, Beyers 110*, note trichomes; F, *L. villosa, Beyers 125*.

Disc

A disc is absent in all species, a state taxonomically significant at the generic level.

Gynoecium

In *Lachnaea* the ovary is sessile, narrowly ellipsoid to ellipsoid, narrowly obovoid to obovoid or narrowly ovoid to ovoid, 0.5–5 mm long, and glabrous or variously pubescent. The ovary is pseudomonomerous—consisting of one expanded or fertile carpel and one contracted or sterile carpel (Heinig 1951; Beyers & Van der Walt 1995), unilocular with a solitary anatropous ovule laterally arising near the top of the ovary, and thus consistent with that of the Gnidieae (Domke 1934). The style arises laterally on the ovary, and is terete to terete-obconical, glabrous or variously pubescent. The stigma is either brush-like, capitate with short or long papillae or conical with short papillae. Zygomorphy is expressed in all species through the lateral position of the style and the single locule.

Fruit

The fruit is an achene which is enclosed in the persistent basal portion of the hypanthium. The pericarp is dry and thin, whereas the seed coat is thick and crustaceous. According to Domke (1934) the achene is, without exception, characteristic of the Thymelaeoideae and the fruit type is therefore not of taxonomic importance at the generic level. In the South African thymelaeaceous genera the pericarp is usually dry, but in *Passerina* it may be dry or fleshy (Bredenkamp & Beyers 2000). The structure of the pericarp is taxonomically significant in *Passerina*, but not in *Lachnaea*.

Discussion

According to Baillon (1880) members of the Thymelaeaceae have numerous constant characters of which the principal ones are: the simplicity of the perianth and its imbricate prefloration; the definite number of parts of the androecium and their insertion on the floral envelope [hypanthium]; the independence of the gynoecium and its insertion inferior to that of the stamens. The characters which vary most and which generally serve to mark the generic divisions are: the number of the parts of the flower; the point of insertion of the stamens and the dimensions of the filaments which render them exserted or enclosed; the presence or absence of scales in the throat of the perianth [hypanthium], and of glands forming a disc at the foot of the gynoecium; the consistence of the pericarp; the mode in which the base of the perianth [hypanthium] falls after floration or persists, enveloping the ripe fruit; the relative proportions of the embryo and the albumen, which may be wanting; and the arrangement of the inflorescence (Baillon 1880).

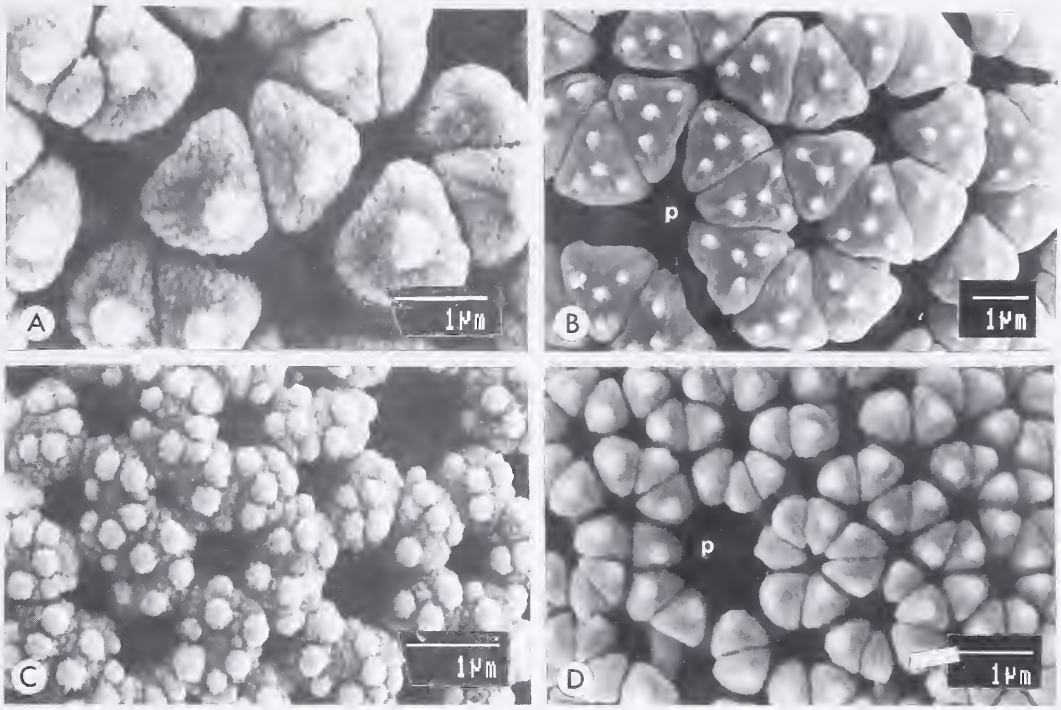

FIGURE 10.—SEM micrographs of parts of pollen grain wall of Thymelaeaceae showing variation of supratectal subunits. A, *Lachnaea gracilis, Bean & Viviers 2613*; B, *Struthiola myrsinites, Beyers 200*; C, *L. pusilla, Beyers 243*; D, *L. leipoldtii, Taylor 10871*. p, pore.

According to Peterson (1959) it is difficult to find reliable characters for generic delimitation in the Thymelaeaceae, as they are few and of superficial significance. In *Gnidia* he found that the number of sepals could be divergent within the same species and that transitions occurred between well-developed and aborted petaloid scales, often within a species. Within *Lachnaea*, however, the number of flower parts is constant, in contrast to Peterson's observation in *Gnidia*.

Floral characters considered taxonomically useful in *Lachnaea* are: the presence or absence of a pedicel; whether the pedicel elongates abaxially beyond the point of insertion of the flower or not; whether the pedicel is persistent and elongates in the fruiting stage; the shape of the upper portion of the hypanthium and whether it narrows into a tube towards the circumscissile articulation or whether it is basally invaginated; whether the calyx is distinctly zygomorphic or not; the colour of the calyx, even though there may be great variability within a species; the position of the stamen insertion and whether the antepetalous stamens are exserted or whether only the anthers of the antepetalous stamens are fully or partially exserted or enclosed; the presence or absence of filament ridges on the hypanthium; whether anthers are with or without broad connective tissue abaxially; the position of the scale insertion on the hypanthium and the shape of the scales; the shape of the stigma and the length of the papillae on it; and the indumentum of the flower.

4.6 PALYNOLOGY

The pollen of the Thymelaeaceae is remarkably uniform: spheroidal, pantoporate and with a *Croton* pattern or a derivative thereof (Nowicke *et al.* 1985). The *Croton* pattern (named by Erdtman 1966) comprises triangular supratectal elements attached to a reticulum (semitectum: Punt *et al.* 1994) with short or irregular columellae (Nowicke 1994). The triangular supratectal elements or subunits may be psilate, striate, furrowed or ridged, or pitted. The subunits may be closely spaced or arrayed in more open configurations (Nowicke 1994).

Discussion

In *Lachnaea* the pollen grains are shed as monads with the structure of the triangular supratectal subunits revealing a similar continuum of variation as described and illustrated for several genera of the Thymelaeaceae by Nowicke *et al.* (1985) and Nowicke (1994), for *Wikstroemia* Endl. by Mayer (1991) and for seven southern African genera of the Thymelaeaceae by Bredenkamp & Van Wyk (1996). The subunits are either tetrahedral with a single central spinule (Figure 10), or flattened with (2–) 4 spinules (Figure 10). Most species of *Lachnaea* have striations on the subunit. When the base-sides of these subunits are emarginate, horizontal intercostal striations also usually occur. Prominent intercostal striations are generally associated with a single central spinule. Few species of *Lachnaea* show a granular pattern on the subunit and these subunits are usually

associated with four spinules, or wart-like structures or verrucae. A continuous range of variation was found between the striate and granular surfaces as well as the number of spinules on the subunits. Variation was not only found amongst species but often within a species or even a specimen. Where several specimens of a species were studied, transitional states of these characters degraded the taxonomic value of these characters.

In the *Lachnaea* species studied, pollen size ranged from 19–67 µm. In three species, viz. *L. nervosa*, *L. greytonensis* and *L. oliverorum* the pollen size varied greatly within a specimen, with the smallest grains less than half or almost half the size of the largest ones. Because of such a wide range, species of *Lachnaea* could not be grouped according to the size of their pollen grains. Polyploidy may express itself directly in pollen size (Muller 1979), but this could not be shown in *Lachnaea*, since the known chromosome number of 18 *Lachnaea* species is the same (n = 9), and no polyploidy is known in the genus. Pollen size in *Lachnaea* can rather be correlated to flower size (Muller 1979) since small flowers were found to have small pollen and larger flowers to have larger grains. Concerning the variation in pollen size (as here recorded in *L. nervosa*, *L. greytonensis* and *L. oliverorum*), Pozhidaev (1993) pointed out that in most palynological investigations, deviant pollen forms are regarded as abnormal and therefore left unregistered, and that published data generally do not reveal the true occurrence of these deviations. Mathew & Valsaladevi (1989) described polymorphism of pollen grains as a state where two or more pollen morphs occur in the same species, or occasionally in a single plant or even the same anther. This polymorphism occurs naturally or due to various factors such as ecological conditions. Mathew & Valsaladevi (1989) and Pozhidaev (1993) also pointed out that deviant pollen forms were found in very different and distant angiosperm groups. As the variation in pollen size in the three *Lachnaea* species was not consistent within a species, the phenomenon could be due to temporary ecological conditions or other factors, but could not be regarded as being well established within the species.

No correlation could be found between either the inflorescence types or the flower morphology and the structure of the supratectal subunits in *Lachnaea*. Just as the size of the pollen grains, the sculpture of the tectum revealed a continuum of variation. Although species could not be grouped according to pollen morphology, the pollen anatomy can assist in some cases in the delimitation of species with similar inflorescences and floral structures. For example, in two closely related species, viz. *L. pusilla* and *L. leipoldtii*, the sculpture of the supratectal subunits can be used as one of the distinguishing characters. In the former species the supratectal subunits are granular with wart-like spinules whereas in the latter the subunits are striate-granular with one or four spinules (Figure 10).

The ultrastructure of the pollen wall reveals a close relationship between *Gnidia* and *Struthiola* because both have very thin footlayers and reduced columellae. *Passerina* shares the reduced columellae with *Gnidia* and *Struthiola*, but the presence of a more prominent footlayer with *Lachnaea* (Beyers & Marais 1998. According to Nowicke *et al.* (1985) the well-developed columellae of *Lachnaea* show a resemblance to those of *Thymelaea arvensis* Lam., *Linodendron cubanum* (A. Rich.) Urb. and *Daphne mezereum* L.

According to Beyers & Marais (1998) the pollen morphology of *Gnidia*, including the species previously placed under *Arthrosolen* and *Lasiosiphon*, is very uniform and has made no contribution to the subdivision of *Gnidia*. The variation in the structure of the tectum in *Gnidia*, *Struthiola* and *Lachnaea* is similarly insignificant. This wider perspective of the palynology of the Cape Flora genera of the Thymelaeaceae convinced the authors that palynology is not an important source of taxonomic evidence for the delimitation of the different genera of the subtribe Gnidiinae, and it did not feature in the decision to include *Cryptadenia* in *Lachnaea*. Nor did pollen analysis contribute much to the delimitation of species in *Lachnaea* or to the grouping of species within the genus (Beyers & Marais 1998). This conclusion corresponds with the results of Heads (1990) for *Kelleria* and *Drapetes* and for the Hawaiian species of *Wickstroemia* (Mayer 1991).

According to Beyers & Marais (1998) the sculpture of the tectum reveals a clear relationship between *Struthiola*, *Gnidia* and *Lachnaea*, and indicates that *Passerina*, in which the supratectal subunits are lacking, stands apart. The closer relationship between *Gnidia*, *Lachnaea* and *Struthiola* supports the placement of these genera in the same subtribe, whereas the distinctly different pollen morphology of *Passerina* supports the classification by Domke (1934), who placed *Passerina* in a separate subtribe, as well as the newly instated tribe Passerineae (Domke) Bredenkamp & Van Wyk (1996).

4.7 CHROMOSOME NUMBER

Most Thymelaeaceae have chromosome numbers of n = 9 and 2n = 18 (Nevling & Woodbury 1966; Sharma & Sarkar 1967, 1968; Bjorkqvist *et al.* 1969; Gupta & Gillett 1969; Kuzmanov 1973; Bhat *et al.* 1974; Loeve & Kjellqvist 1974; Majovsky *et al.* 1974; Heads 1990; Beyers & Van der Walt 1995). Polyploidy has been recorded in *Daphne* L. (Heads 1990), *Daphnopsis* C. Mart. (Nevling & Woodbury 1966), *Edgeworthia* Meisn. (Heads 1990) and *Wikstroemia* (Gupta & Gillett 1969; Heads 1990).

Observations

Chromosome counts for 18 species of *Lachnaea* are now known (Table 4); in all cases they are n = 9. *Beyers 125* (NBG) referred to as *L. funicaulis* in Beyers & Van der Walt (1995) was misidentified. It is the new species, *L. villosa* Beyers described on p.87.

Discussion

Since the basic chromosome number of n = 9 was recorded for most genera of the Thymelaeaceae, the chromosome number is taxonomically insignificant at the generic and specific levels.

5. Phytogeography

The Cape Floristic Region (CFR) is a highly distinctive phytogeographical unit, which is recognized as one of the six floral kingdoms of the world (Good 1974; Goldblatt 1978; Takhtajan 1986). The CFR as defined by Goldblatt (1978) includes the territory west and south of a line extending from Nieuwoudtville in the north, following the eastern slopes of the Cederberg, and then east from Karoopoort along the northern slopes of the Witteberg, Swartberg, Baviaans Kloof, and Groot Winterhoek Mountains, ending at Port Elizabeth (Goldblatt 1978). The region has a relatively mild, temperate, mediterranean-type climate. Rainfall occurs predominantly or entirely in the winter, but the eastern part receives substantial summer rain. The rainfall pattern is orographic; precipitation increases with altitude, and rain shadow effects are more than usually pronounced. The surface area of the CFR is small, ± 90 000 km^2, less than 4% of the area of southern Africa. The species diversity, about 9 000 species of vascular plants, constitutes about 44% of the total flora of southern Africa (Goldblatt & Manning 2000). For equivalent-sized areas, this region has the highest recorded plant species diversity for any temperate region in the world (Cowling 1992). Taylor (1980) includes the Thymelaeaceae among those families that are richest in genera in the Cape Region but widely distributed in other parts of the world. Perhaps more remarkable than species diversity of the CFR is the degree of endemism, which is 68.2 % for species and 19.5 % for genera (Bond & Goldblatt 1984). Weimarck (1941) was the first to recognize centres of endemism in the CFR. He recognized five centres, which formed the basis for the analysis of distribution patterns for many subsequent monographs (e.g. Dahlgren 1963; Nordenstam 1969; Lundgren 1972; Strid 1972). These centres are also supported by the studies of Oliver *et al.* (1983). Weimarck failed to recognize a well-defined centre associated with the limestones of the southwestern and southeastern coastal region which Cowling (1992) calls the Bredasdorp-Riversdale Centre. Thus at present the CFR constitutes six centres of endemism, viz. Northwestern (NW), Southwestern (SW), Bredasdorp-Riversdale (BR) (the Agulhas Plane Centre of Goldblatt & Manning 2000), Karoo Mountain (KM), Langeberg (LB) and Southeastern (SE) Centres.

OBSERVATIONS

The genus *Lachnaea* is endemic to the CFR. *Lachnaea* species occur almost exclusively in fynbos vegetation on oligotrophic soils derived from the orthoquartzites of the Cape Supergroup. A few species, however, occur on shale or limestone. The number of species found per quarter degree and per degree square, coded according to the grid reference system of Edwards & Leistner (1971), is illustrated in Figures 11 and 12. The highest number of species (24) occurs in the 3319 (Worcester) grid, with the highest diversity of species (12) in the Hex River Mountains (3319AD), followed by the Groot Winterhoek Mountains (3319AA) with 11 species. Species richness of the genus declines to the north, south, east and west of the above concentration of species.

On a regional basis there is a conspicuous concentration of species in the Northwestern Centre. Twenty-one of the 40 recognized species occur here of which the following 12 are endemic (Table 14): *L. alpina*, *L. filamentosa*, *L. funicaulis*, *L. laniflora*, *L. leipoldtii*, *L. marlothii*, *L. montana*, *L. naviculifolia*, *L. pedicellata*, *L. pendula*, *L. striata* and *L. villosa*. Most of these species are found at altitudes from 1 000 m upwards, with *L. marlothii* and *L. montana* occurring at altitudes as high as 2 330 m in the Hex River Mountains. *L. filamentosa* has been recorded from 600–1 900 m, *L. striata* from 800–1 160 m, *L. villosa* from 480–1 500 m and *L. funicaulis* from 500–1 000 m. These species are essentially montane although some grow on flats and lower mountain slopes.

Of the 18 species occurring in the Southwestern Centre, five are endemic to that Centre, viz. *L. greytonensis*, *L. laxa*, *L. pudens*, *L. pusilla* and *L. rupestris*. They are all found on sandstone slopes. *L. greytonensis* and *L. pudens* occur on the Riviersonderend Mountains at altitudes between 640–830 m and 330–1 530 m respectively. *L. rupestris* is found on the Riviersonderend Mountains to Stettynsberg north of Villiersdorp, growing amongs rocks at altitudes above 1 500 m. *L. laxa* has been recorded from the Jonkershoek Mountains to the Swartberg in the Caledon District and Elim at altitudes between 600–2 150 m. *L. pusilla* occurs in the Elandskloof Mountains at altitudes between 70–1 000 m.

Only one of the six species represented in the Karoo Mountain Centre, *L. oliverorum*, is endemic to that Centre. It is restricted to the Waboomsberg in the Montagu District growing on sandy soil at altitudes between 1 280–1 400 m.

Of the 14 species represented in the Langeberg Centre, four are endemic: *L. ericoides*, *L. penicillata*, *L. sociorum* and *L. stokoei*. *L. stokoei* is known only from two Stokoe collections: Lemoenshoek dated December 1954 and Strawberry Hill near Barrydale dated January 1957. Unfortunately the localities given on the sheets are very vague and no other more recent information is available about this species. *L. ericoides* and *L. penicil-*

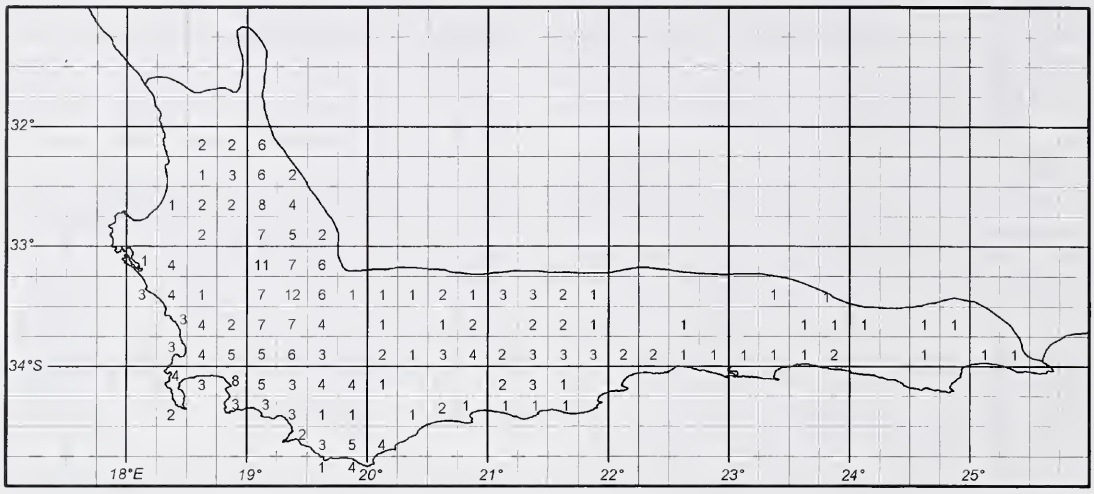

FIGURE 11. Distribution of genus *Lachnaea* with number of species per quarter degree grid square. Inland boundary of Cape Floristic Region following Goldblatt (1978).

lata occur west of the Gourits River at altitudes between 330–660 m and 300–1 330 m respectively. *L. sociorum* is found on the eastern end of the region on either side of the Gourits River at altitudes between 300–1 000 m. All three species occur on sandstone slopes.

There are no endemic species of *Lachnaea* in either the Bredasdorp-Riversdale or Southeastern Centre. However, five species occur in the Bredasdorp-Riversdale Centre and three in the Southeastern Centre.

The two allopatric subspecies of *L. globulifera* are both endemic to two adjacent centres: subsp. *globulifera* to the Southwestern Centre and subsp. *incana* to the Northwestern Centre.

Among the *Lachnaea* species, diverse types of distributions occur. *L. greytonensis*, *L. funicaulis*, *L. leipoldtii*, *L. marlothii*, *L. pudens*, *L. pusilla*, *L. rupestris* and *L. stokoei* can be regarded as being narrowly endemic. These species are either found in a single locality or restricted to adjacent localities in a small area. *L. axillaris*, *L. macrantha*, *L. montana* and *L. striata* all have a disjunct distribution: *L. axillaris* occurs on sandy flats in the vicinity of Hopefield and Darling, in the southwestern area, and reappears along the southern coast from

FIGURE 12. Distribution of genus *Lachnaea* with number of species per degree grid square. Inland boundary of Cape Floristic Region following Goldblatt (1978).

TABLE 14.—Species of *Lachnaea* represented in centres of endemism of Cape Floristic Region

Species	Centres of endemism					
	NW	SW	B-R	KM	LB	SE
alpina	✳					
aurea		×	×			
axillaris		×	×		×	
burchellii					×	×
capitata	×	×				
densiflora		×	×			
diosmoides					×	×
elsieae	×			×		
ericoides					✳	
eriocephala	×	×				
filamentosa	✳					
filicaulis		×	×		×	
funicaulis	✳					
globulifera	×	×				
glomerata				×		×
gracilis	×	×		×		
grandiflora	×	×	×			
greytonensis		✳				
laniflora	✳					
laxa		✳				
leipoldtii	✳					
macrantha		×			×	
marlothii	✳					
montana	✳					
naviculifolia	✳					
nervosa	×	×			×	
oliverorum				✳		
pedicellata	✳					
pendula	✳					
penicillata					✳	
pomposa	×	×		×		
pudens		✳				
pusilla		✳				
rupestris		✳				
ruscifolia				×	×	
sociorum					✳	
stokoei					✳	
striata	✳					
uniflora	×	×				
villosa	✳					
TOTAL	21	18	5	6	11	3

✳ species endemic to one centre; NW, Northwestern; SW, Southwestern; B-R, Bredasdorp-Riversdale; KM, Karoo Mountain; LB, Langeberg; SE, Southeastern.

Elim to the Gourits River mouth; *L. macrantha*, a species with a localized distribution, is found in the mountains in the Southwestern Centre and then on the Langeberg in the Swellendam and Riversdale Districts; *L. montana* occurs on the Piketberg, Hex River Mountains and Keeromsberg, and *L. striata* has been recorded from the Northern Cederberg and then again from the Groot Winterhoek and Witzenberg Mountains in the vicinity of Tulbagh. With the exception of *L. axillaris*, these species are all montane species. The distribution of a few *Lachnaea* species may be termed wide or fairly wide when extending over three centres as in *L. filicaulis*, *L. grandiflora* and *L. pomposa*.

CONCLUSION

Oliver *et al.* (1983) plotted the distribution of all species of Restionaceae, Ericaceae and Proteaceae known from the CFR. Their maps revealed six phytogeographical centres which agree essentially with those of Weimark (1941). They also determined that one of the major phytogeographical patterns in the Cape Flora is a concentration of species and diversity in the mountains of the southwestern Cape with the number of species per unit area decreasing from this centre. They found the quarter degree, 3418 BB centred on Sir Lowry's Pass and the Hottentots Holland Mountains to be the richest area in the CFR. The highest concentration of species in the genus *Metalasia* R.Br. is also nested in the western Caledon area in the 3418 grid (Karis 1989). A similar pattern is found in *Aspalathus* (Dahlgren 1969), *Cliffortia*, *Muraltia* and many other genera (Nordenstam 1969). In the genus *Pelargonium* L'Hérit. the 3319 (Worcester) and 3318 (Cape Town) grids were found to have the highest concentration of species (Van der Walt & Vorster 1983). In *Lachnaea*, the quarter degree, 3319 AD in the Worcester grid was found to house the highest number of species.

Lachnaea demonstrates a high percentage of regional endemism with 55% of the species endemic to one of four of the centres in the CFR. Most of these species can be regarded as montane species. The relief and terrain diversity of the Cape Fold Mountains, in combination with edaphic factors and the climate regime, are part of the understanding why upland centres of species richness occur and have persisted in the Cape mountains (Cowling 1992).

6. Cladistic analysis and speciation

CLADISTIC ANALYSIS

Cladistic analysis of the southern African Gnidieae, as defined by Domke (1934), has not previously been attempted. At present, molecular studies of the Thymelaeaceae are being undertaken (M. van der Bank pers. comm.); results are likely to have a direct bearing on the classification of this family. Preliminary results from the sequencing of the plastid genes, *rbc*L and *trn*L, support the monophyletic status of *Lachnaea* (M. van der Bank pers. comm.).

Choice of outgroup

In Domke's (1934) classification of the Thymelaeaceae, *Lachnaea*, *Gnidia s. str.* and *Struthiola* are placed in the same subseries within the subtribe Gnidiinae, thus reflecting his view of their close affinity. Recently, preliminary cladistic analysis based on sequence data from the *rbc*L gene has shown *Struthiola leptantha* Bolus to be basal to the clade which includes *Lachnaea filicaulis*, *Passerina filiformis* L., *Gnidia denudata* Lindl. and *G.* aff. *renniana* Hilliard & B.L.Burtt (Van der Bank pers. comm.). According to Van der Bank the genus *Gnidia* appears to be polyphyletic. Nixon & Carpenter (1993) stated that if the outgroup is the sister group, the cladistic inference might be better founded and that the more outgroups used, the better founded the inference might be. Consequently *S. leptantha* and five *Gnidia* species, namely *G. galpinii* C.H.Wright, *G. linearifolia* (Wikstr.) B.Peterson, *G. oppositifolia* L., *G. pinifolia* L. and *G. squarrosa* (L.) Druce, were chosen as outgroups in Analysis B (Figure 14).

Choice of characters and data matrices

Morphological data for *Lachnaea* were assembled from the present study, whereas those for the *Gnidia* species and *S. leptantha* were obtained from literature and dried material at NBG. Leaf anatomical data for the *Gnidia* species were based on hand sections made from rehydrated herbarium material at NGB and those for *S. leptantha* from Van der Merwe (1992). Information on floral and inflorescence morphology of *Struthiola* was obtained from Mattatia (1965).

In selecting the morphological data, consideration was given to continuous versus discrete and overlapping versus non-overlapping characters (compare Stevens 1991; Thiele 1993; Wiens 1995). Since the HENNIG86 version 1.5 (Farris 1988) does not distinguish between polymorphic and unknown characters, it was decided to exclude the polymorphic ones following Thiele (1993). All assumptions regarding the direction of transformation series were considered inappropriate prior to analysis (Hauser & Presch 1991) and multistate characters were treated as unordered. Ultimately 33 discrete characters were selected (Table 15) which is a small number considering the number of taxa analysed. Unfortunately only a small number of diagnostic characters were found in *Lachnaea*.

Analysis of data matrix

The mh* and bb* options of the HENNIG86 package were used. The data include considerable homoplasy with the result that in the first analysis (Analysis A), with only *S. leptantha* as outgroup, the strict consensus tree of 2282 (overflow) equally parsimonious trees, resulting from unweighted computations, shows little resolution [length 113, consistency index (CI) 0.31, retention index (RI) 0.71] (Figure 13). Similarly in the second analysis (Analysis B), with multiple taxa as the outgroup, the strict consensus tree of 2044 (overflow) trees (length 135, CI 0.27, RI 0.69) also showed little resolution (Figure 14). Therefore successive weighting (xsteps w), as recommended by Farris (1969), was applied in both analyses. In Analysis A character 17 was excluded as it is an autapomorphy for *L. axillaris*, whereas in Analysis B all the characters in the matrix were included. Clados (Nixon 1993) was used to look at character distribution on the HENNIG86 trees. Two types of character transformations were plotted: unique occurrences (synapomorphies) in black and homoplasies (forward or reverse homoplasy) in grey. The bootstrap option in HENNIG86 was run on 1000 replicates using mh*and bb* options to establish a measure of confidence in the results of the cladistic analysis. The bootstrap values are indicated on the initial two trees (Figures 13; 14).

Results

Analysis A produced 2274 (overflow) equally parsimonious trees, 269 steps long, CI 0.68 and RI 0.91, whereas in Analysis B, 2044 (overflow) equally parsimonious trees, 248 steps long, CI 0.58 and RI 0.88 were produced. The strict consensus tree of each analysis (Figures 15; 16) shows that *Lachnaea* is monophyletic, characterized as a genus by the insertion of the floral scales below the stamen attachment [22(1)] in Analysis B and the presence of the antesepalous stamen whorl [19(0)] in Analysis A.

Analysis A (Figure 15)

Within *Lachnaea*, the tree indicates a primary division into two basal clades. One basal clade comprises eight of the ten solitary-flowered species. These are

TABLE 15.—Matrix and character list for cladistic analysis (Figures 12–15). Outgroups are five *Gnidia* species and *Struthiola leptantha*. No polarity is implied in allocation of character states. Multistate characters were treated as unordered. Genera: G, *Gnidia*; L, *Lachnaea*; S, *Struthiola*

Taxon	Character numbers						
	1–5	6–10	11–15	16–20	21–25	26–30	31–33
G. galpinii	01101	10100	– 0100	00010	00000	00100	?00
G. linearifolia	00011	00100	– 0100	01010	00000	02110	100
G. oppositifolia	01001	00100	– 0100	01111	00000	00100	?00
G. pinifolia	00001	00303	00100	01011	00000	02010	?00
G. squarrosa	00011	10100	– 0100	01111	00000	00100	?01
S. leptantha	01000	20400	– 00–1	01101	00000	00100	000
L. alpina	00101	01000	– 00–1	01110	01100	10100	100
L. aurea	00101	00303	01101	01110	01101	10100	010
L. axillaris	11100	10400	– 00–0	10011	11201	01010	100
L. burchellii	01101	10100	– 0101	01210	01101	10100	000
L. capitata	00001	01000	– 00–0	01110	11200	10110	000
L. densiflora	00001	01000	– 00–0	01110	01200	10110	000
L. diosmoides	00101	00100	– 0101	01110	01101	11010	000
L. elsieae	11121	10220	– 0111	01110	01101	01110	001
L. ericoides	00121	10100	– 0101	01010	01101	11110	100
L. eriocephala	11111	00220	– 1211	01110	01100	10110	001
L. filamentosa	00001	01000	– 10–1	01110	01100	10100	100
L. filicaulis	01100	10400	– 00–0	01111	11201	02010	000
L. funicaulis	11111	10302	10111	01110	11201	01010	001
L. globulifera	11101	10311	10211	01110	01100	10110	001
L. glomerata	01101	10100	– 0101	01110	01101	11110	000
L. gracilis	01100	10400	– 00–0	01111	11201	01000	100
L. grandiflora	01100	00400	– 00–0	01110	11211	01110	100
L. greytonensis	11111	10220	– 0111	01110	11201	01010	001
L. laniflora	11101	00220	– 0101	01110	01101	10110	001
L. laxa	01100	00400	– 00–1	01210	01100	10110	000
L. leipoldtii	11100	00400	– 00–0	11010	11201	02011	001
L. macrantha	00101	01000	– 10–1	01110	01100	10100	000
L. marlothii	11101	00220	– 0111	01010	01101	01110	001
L. montana	11101	10311	00211	01110	01100	10110	001
L. naviculifolia	11101	01220	– 0211	01111	01101	10110	100
L. nervosa	00101	10100	– 0101	01210	01100	10110	100
L. oliverorum	11111	10302	10111	01110	11201	01110	001
L. pedicellata	11101	10311	00211	01110	01101	10110	001
L. pendula	11121	00302	10111	01110	01101	11110	001
L. penicillata	11111	00302	10111	01110	01101	11111	001
L. pomposa	00001	01000	– 00–1	01110	01100	10100	100
L. pudens	01100	10400	– 00–0	11111	11201	00111	101
L. pusilla	11100	00400	– 00–0	11211	11201	02010	001
L. rupestris	11101	10220	– 0211	01110	01101	10110	001
L. ruscifolia	00110	20400	– 00–1	01110	01101	11110	100
L. sociorum	00101	00100	– 0101	01010	01101	10110	100
L. stokoei	00121	00100	– 0100	01110	11111	11100	100
L. striata	00111	00100	– 0101	01010	01100	10100	010
L. uniflora	01100	00400	– 00–0	01110	11211	02110	000
L. villosa	11111	10220	– 0111	01110	01101	01111	001

? unknown; – inapplicable.

Character list

1. Branches ridged below leaf base (0); not ridged below leaf base (1)
2. Leaf arrangement: alternate (0); opposite (1)
3. Leaves: amphistomatic (0); epistomatic (1).
4. Leaf margin: eciliate (0); ciliate (1); apex with tuft of hairs (2)
5. Inflorescence class: monotelic (0); polytelic (1)
6. Inflorescence position: on main flowering branches (0); on main flowering branches and on short lateral flowering branches (1); only on reduced lateral branches (2)
7. Inflorescence: sessile (0); pedunculate (1)
8. Type of inflorescence: capitulum (0); ebracteate umbel (1); pseudobracteate umbel (2); bracteate umbel (3); solitary-flowered (4)
9. Distal leaves subtending inflorescence: leaf-like (0); bract-like: 2 (1); 4–6 (2)
10. Involucral bracts: 0 (0); 2 (1); 4 (2); 6–8 (3)
11. Margin of involucral bracts: glabrous (0); ciliate (1)
12. Flower symmetry: subactinomorphic (0); zygomorphic (posterior sepal at least half length of anterior sepal) (1)
13. Pedicel: absent (0); present, abaxially not produced beyond flower attachment (1); present, abaxially produced beyond flower attachment (2)
14. Pedicel: not elongating in fruit (0); elongating in fruit (1)
15. Upper portion of hypanthium: not stalked (0); stalked (1)
16. Upper portion of hypanthium: without basal invagination (0); with basal invagination (1)
17. Indumentum of upper portion of hypanthium outside: glabrous (0); hairy: trichomes acicular (1)
18. Indumentum of basal portion of hypanthium outside: glabrous (0); hairy: trichomes acicular (1); hairy: trichomes obtuse (2)
19. Antesepalous stamen whorl: absent (0); present (1)
20. Anthers abaxially with broad connective tissue: absent (0); present (1)
21. Floral scales: exserted (0); included (1)
22. Floral scale insertion: above stamen attachment (0); below stamen attachment (1)
23. Position of floral scales on upper hypanthium: rim (0); above midway (1); below midway (2)
24. Scale attachment to hypanthium wall: basally (0); abaxially (1)
25. Style shape: terete (0); terete-obconical (1)
26. Style indumentum: glabrous (0); pubescent (1)
27. Stigma shape: penicillate (0); capitate (1); conical (2)
28. Stigmatic papillae: short (0); long (1)
29. Leaf shape, abaxially: plane (0); convex (1)

Leaf anatomy:

30. Stomata position relative to adjacent epidermal cells: sunken (0); level (1)
31. Diosmin crystals: absent (0); present (1)
32. Extraxylary fibres along lateral margin: absent (0); present (1)
33. Extraxylary fibres capping lateral vascular bundles: well developed (0); weakly developed (not more than two fibres present) (1)

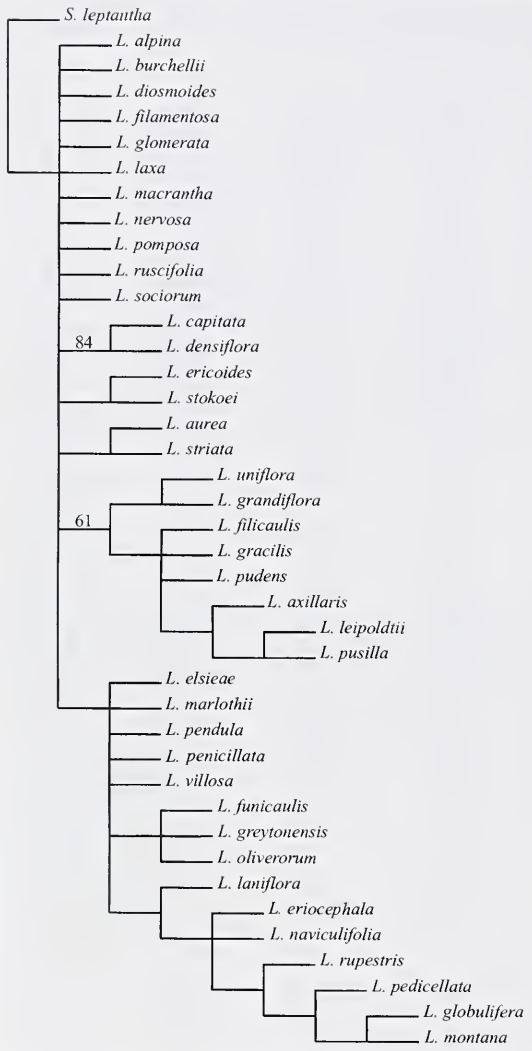

FIGURE 13.—Strict consensus tree generated from character matrix (Table 15) excluding character 17, with only *Struthiola leptantha* as outgroup and using mh* and bb* options of HENNIG86. Bootstrap values drawn on strict consensus tree generated using mh* and bb* options of HENNIG86. L, *Laclnaea*; S, *Strutliiola*.

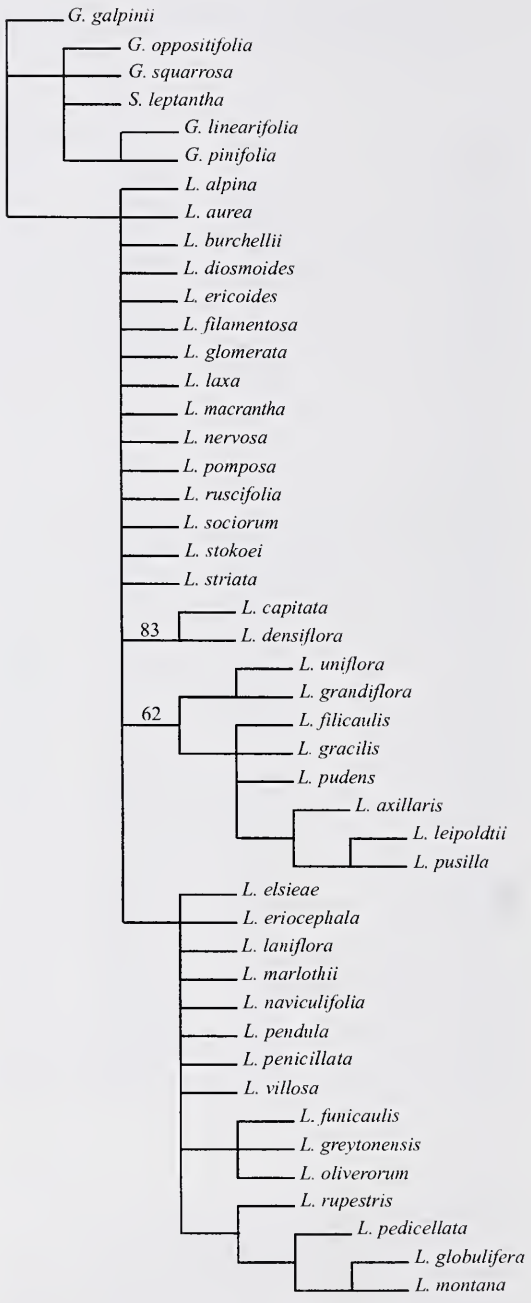

FIGURE 14.— Strict consensus tree generated from character matrix (Table 15) with multiple taxa as outgroup and using mh* and bb* options of HENNIG86. Bootstrap values drawn on strict consensus tree generated using mh* and bb* options of HENNIG86. G, *Gnidia*; L, *Laclnaea*; S, *Strutliiola*.

supported by five homoplasious characters, namely, the upper portion of the hypanthium unstalked [15(0)], the floral scales included [21(1)], arising below midway in upper portion of the hypanthium [23(2)], a terete-obconical style [25(1)] and a capitate stigma [27(1)]. However, within this group all the species do not share a capitate stigma. A conical stigma [27(2)] occurs in four species and a penicillate one [27(0)] in one species. The terminal group in this clade is held together by a synapomorphy, namely the upper portion of the hypanthium with basal invagination [16(1)].

The other basal clade, supported by two homoplasies, namely, scales inserted above midway up hypanthium [23(1)] and pubescent style [26(1)], includes the rest of the species. *L. laxa* and *L. ruscifolia*, the two other solitary-flowered species, are included in this clade and are basal. The rest of the species are held together by a synapomorphy (polytelic inflorescences [5(1)]). Here this subclade branches dichotomously with *L. alpina*, *L.*

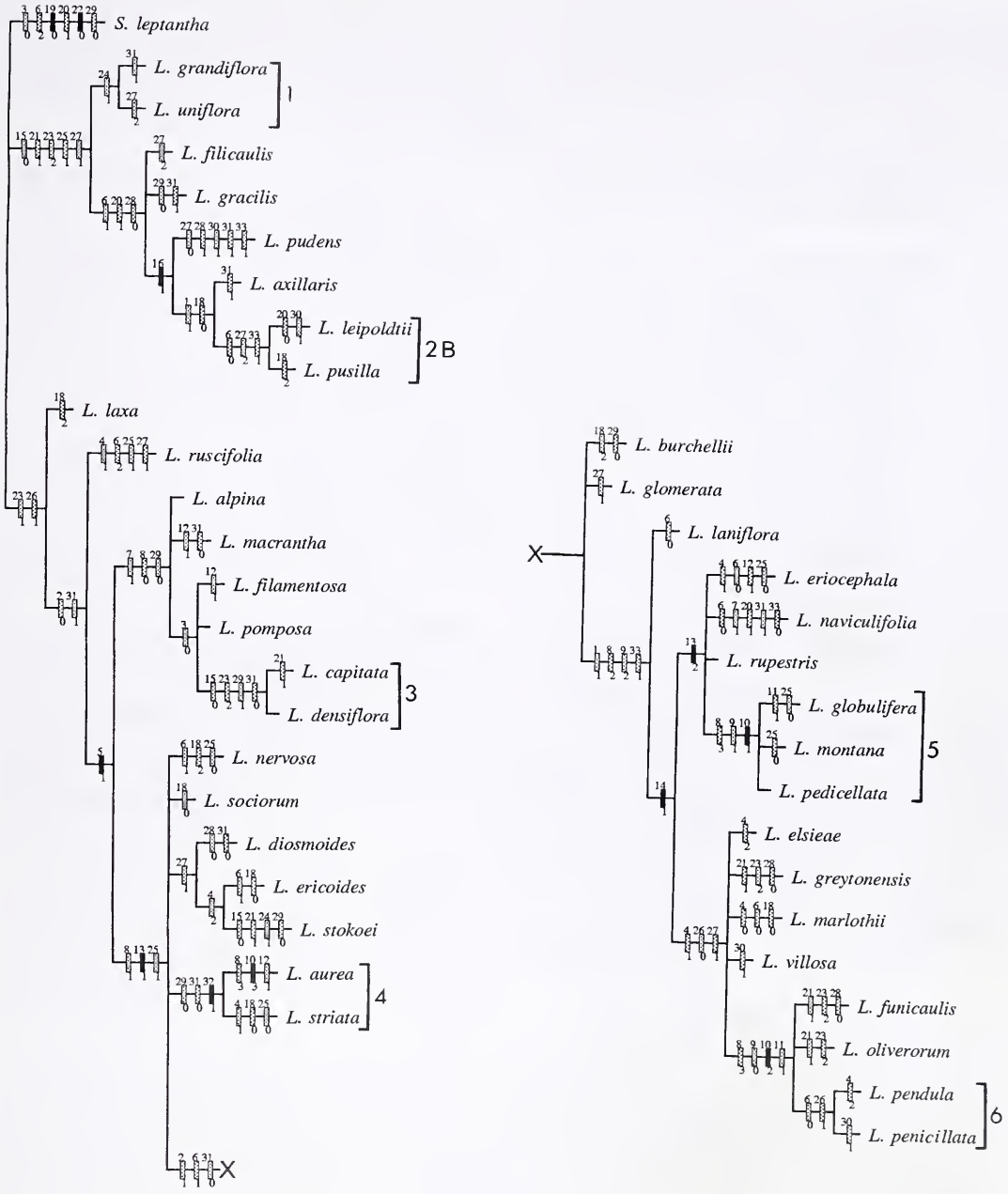

FIGURE 15.—Analysis A. Strict consensus tree generated from character matrix (Table 15) excluding character 17, with only *Struthiola leptantha* as outgroup and using mh*, bb* and successive weighting (xsteps w) options of HENNIG86. Character bars mapped onto tree are shaded as follows: black, synapomorphic character; gray, homoplasious character. Numbers above character bars refer to character numbers, those below bars indicate character state. L, *Lachnaea*; S, *Struthiola*.

macrantha, *L. filamentosa*, *L. pomposa*, *L. capitata* and *L. densiflora* included in a subclade. This subclade is supported by pedunculate [7(1)] capitula [8(0)] and leaves abaxially plane [29(0)]—this character reverses further up the subclade [29(1)] in *L. capitata* and *L. densiflora*. The subclade with *L. filamentosa*, *L. pomposa*, *L. capitata* and *L. densiflora* is held together by a secondary derived character (also present in outgroup), namely, amphistomatic leaves [3(0)]. The second subclade in the dichotomy is supported by two homoplasies [8(1) and 25(1)] and a synapomorphy (pedicels present [13(1)]). All the species in this subclade have umbellate inflorescences. This subclade is polychotomous. Here a well-defined subgroup can be distinguished by a synapomor-

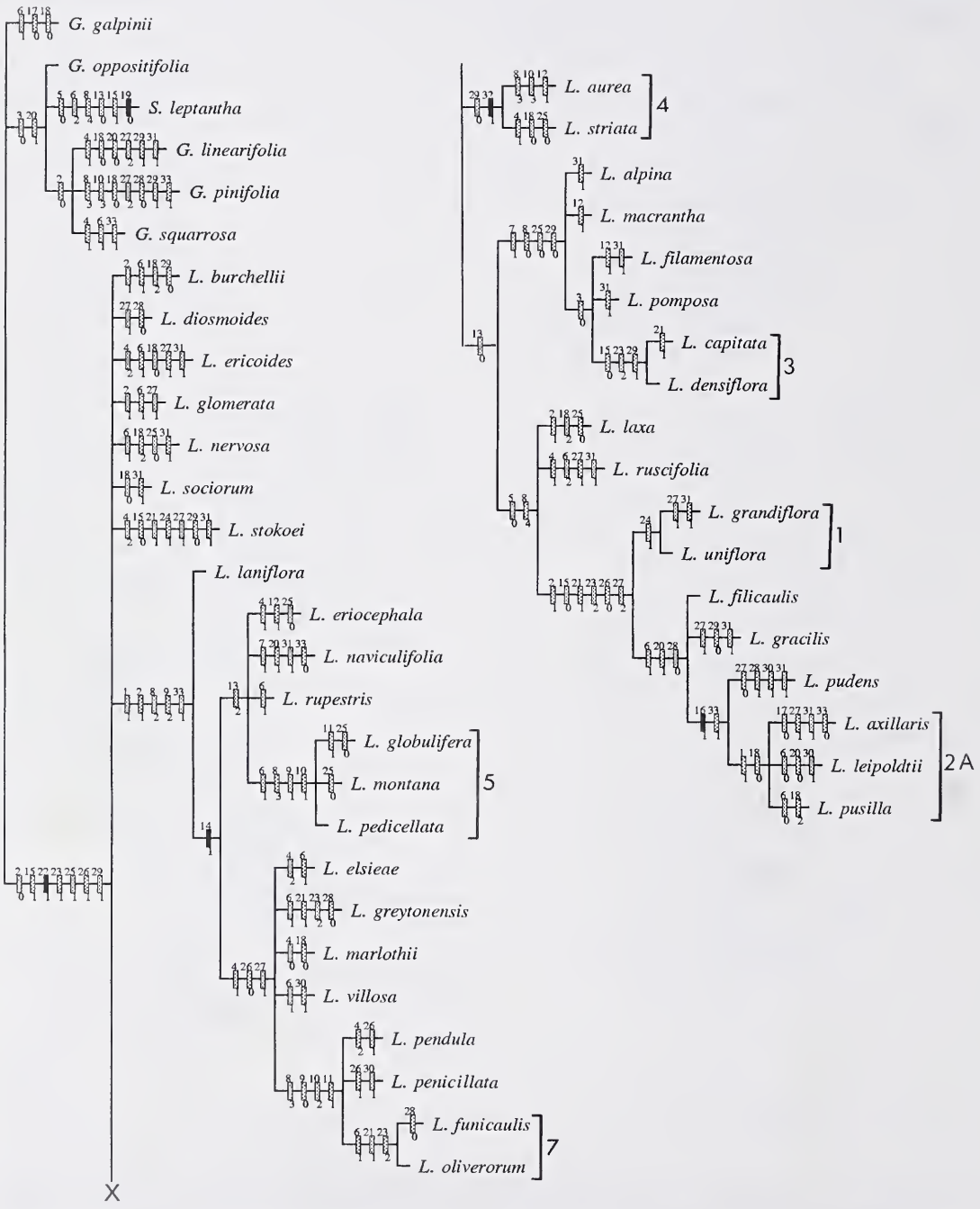

FIGURE 16.—Analysis B. Strict consensus tree generated from character matrix (Table 15) with multiple taxa as outgroup and using mh*, bb*, and successive weighting (xsteps w) options of HENNIG86. Character bars mapped onto tree are shaded as follows: black, synapomorphic character; gray, homoplasious character. Numbers above character bars refer to character numbers, those below bars indicate character state. G, *Gnidia*; L, *Lachnaea*; S, *Struthiola*.

phy (pedicels elongating in fruit [14(1)]. Within this subgroup a further group of species is distinguished by another synapomorphy (pedicels abaxially produced beyond flower attachment [13(2)]).

Analysis B (Figure 16)

The clade containing all the *Lachnaea* species is polychotomous. The well-defined groups of species,

however, are rather similar to those indicated by the previous analysis. One of the major differences is that all the solitary-flowered species are grouped together in one clade supported by monotelic [5(0)] solitary-flowered [8(4)] inflorescences.

Discussion

Meisner (1840) subdivided *Lachnaea* into three sections, *Sphaeroclinium*, *Conoclinium* and *Microclinium*, based mainly on the inflorescence morphology. In a subsequent publication the same three sections were recognized with a few alterations (Meisner 1857). The section *Sphaeroclinium* is defined by terminal capitula with flowers on a globose, sessile receptacle. Within this section he distinguished two subsections, *Exinvolucratae* and *Involucratae*. He placed *L. filamentosa*, *L. macrantha* and *L. pomposa* (= *L. buxifolia*), within the *Exinvolucratae*. The placement of these three species is supported by the cladistic analysis. In his *Involucratae* he included *L. aurea*, *L. burchellii*, *L. eriocephala*, *L. globulifera* and *L. nervosa* (= *L. ambigua*). These species, however, come out in different clades and Meisner's arrangement can therefore not be supported.

Section *Conoclinium* was defined by Meisner (1857) as having terminal or subterminal, exinvolucrate capitula with few or many flowers borne on a slightly thick conical to hemisperical, tomentose, tuberculate receptacle which later elongates and becomes cylindrical. Here he includes *L. alpina*, *L. capitata*, *L. densiflora* and *L. striata*. The first three species are contained in the same clade as those in his *Exinvolucratae* whereas *L. striata* comes out in a clade with *L. aurea*.

In section *Microclinium* the flowers are sessile, terminal or subsolitary, rarely axillary and solitary, without an involucre and receptacle. Species included are *L. axillaris*, *L. diosmoides*, *L. ericoides*, *L. gracilis*, *L. uervosa* and *L. penicillata*. These species come out in different clades and thus *Microclinium* can not be regarded as a natural section.

Unfortunately Meisner (1840, 1857) misinterpreted the inflorescence morphology and consequently considered all the flowers to be sessile. In both analyses the pedicel characteristics are significant. The solitary-flowered species, he regarded as having axillary inflorescences. Therefore the criteria used to define his sections can not be accepted.

Conclusion

The two analyses produced conflicting resolution regarding the solitary-flowered species. In Analysis A, *L. laxa* and *L. ruscifolia* are embedded basally in one of the basal clades whereas in Analysis B they are included with the other solitary-flowered species in a distal subclade. All attempts to meaningfully resolve the polytomy in the two analyses with the morphological data at hand, failed. A more meaningful analysis would be to run morphological data together with evidence from other sources (e.g. molecular data). With the evidence at hand, *Lachnaea* cannot be subdivided into sections and the three sections proposed by Meisner (1840, 1857) are not upheld.

With the cladograms containing so much homoplasy it is difficult to develop with any certainty a hypothesis on the evolution of many of the characters.

In analysis A, there are some indications of the direction of evolution in inflorescence characters. The monotelic inflorescence is plesiomorphic and the polytelic inflorescence apomorphic. The umbellate inflorescence appears to have evolved from the ebracteate to the bracteate state. The number of bracts (2, 4, 4–6) has arisen independently in different lineages. In analysis B the polytelic inflorescence is plesiomorphic. The monotelic inflorescence is a parallelism, occurring in one of the outgroups (*S. leptantha*) as well as in the ingroup. The results from the two analyses support the conclusion of Weberling & Herkommer (1989) who found that within the Gnidioideae certain taxa have monotelic inflorescences, and that it was impossible to draw any taxonomic conclusion exclusively from the existence of the monotelic type within those taxa. The polytelic inflorescence has probably been derived repeatedly from the monotelic type (Weberling 1983).

The multistate character [13]: pedicel absent (0); present, abaxially not produced beyond flower attachment (1); present, abaxially produced beyond flower attachment (2); is clearly an evolutionary advancement in Analysis A. In Analysis B pedicels present, abaxially not produced beyond flower attachment [13(1)] is plesiomorphic, and pedicels abaxially produced beyond flower attachment [13(2)] is apomorphic. Pedicel absent [13(0)] is a parallelism occurring in *S. leptantha* and in the ingroup holding the capitate and solitary-flowered species together in a clade. Pedicel elongating in fruit [14(1)] is a derived condition in both analyses.

Two other characters showing evolutionary advancement in both analyses are characters 16 and 32. The upper portion of the hypanthium with basal invagination [16(1)] is a synapomorphy for *L. pudens*, *L. axillaris*, *L. leipoldtii* and *L. pusilla*. Extraxylary fibres present along lateral margins of leaves [32(1)] supporting the clade with sister species, *L. aurea* and *L. striata*, is a derived condition.

The evolution of the strongly zygomorphic flowers of *L. aurea*, *L. eriocephala*, *L. filamentosa* and *L. macrantha*, a derived condition occurring in different lineages, was probably pollinator-driven.

The cladistic analysis (Analysis A) forms the basis of the arrangement of species in the formal taxonomic treatment (Chapter 7). Since the cladogram represents the first cladistic analysis of *Lachnaea* based on morphological data, the hypothesis of relationships presented here should be seen as a starting point and by no means as the final word.

TABLE 16.—Comparison of life history traits in seven terminal species pairs/triplets emanating from cladograms in Figures 14 & 15

Species pairs/triplets		1	2A	2B	
Species	*L. grandiflora*	*L. uniflora*	*L. axillaris*	*L. leipoldtii*	*L. pusilla*
Soil	sandy	sandy, stony	sandy	sandy	sandy, stony
Distribution	Swartboskraal in Clanwilliam Dist. south and southeast to Cape Peninsula, Bredasdorp, and inland: Citrusdal to Worcester	Darling to Cape Peninsula and Somerset West and inland: Twenty-four River Mtns, Wolseley, Franschhoek	Hopefield, Darling; Elim to Gourits River mouth	Northern Cederberg (alt.: 1 000 m)	Nuwekloof southwest of Tulbagh, along Elandskloof to Bailey's Peak north of Wellington
Flowering time	all year except July	July–March	all year	December, February	October–March
Habitat	sandy flats, lower mountain slopes	Form A, sandy flats; B, mountain slopes	sandy flats, limestone ridges	moist, sandy flats	restioid, sandy flats
Flower colour	pink, pinkish mauve, white	pink, pinkish mauve, occ. white	cream, pink, dark pink	white	white, some tinged pink
Regeneration	resprouter	A, reseeder B, resprouter	resprouter	reseeder	reseeder

Species pairs/triplets		3	4
Species	*L. capitata*	*L. densiflora*	*L. aurea*	*L. striata*
Soil	sandy	sandy	sandy	sandy
Distribution	Clanwilliam to Cape Peninsula, and inland: Franschhoek, Goudini	southern Cape Peninsula to Bredasdorp	Hermanus to Agulhas (alt.: below 900 m)	Northern Cederberg, Grootwinterhoek, Witsenberg, Roodesand Mtns
Flowering time	June–March	August–March	March–September	September–January
Habitat	sandy flats, lower mountain slopes	sandy flats	flats and lower mountain slopes	mountain slopes, seasonally damp areas
Flower colour	cream	cream, pink, dark pink	golden yellow	cream, pale rose, purple
Regeneration	reseeder	reseeder	resprouter	resprouter

Species pairs/triplets		5	6			7
Species	*L. globulifera*	*L. montana*	*L. pedicellata*	*L. pendula*	*L. penicillata*	*L. funicaulis*	*L. oliverorum*
Soil	sandy; sandy stony	stony; sandy	sandy, loam probably on underlying shale	stony	sandy or stony clay	sandy	sandy
Distribution	Pakhuis Mtn to Bainskloof, Du Toit's Kloof, Stettyn Mtn (alt.: 200–1 665 m)	Piketberg Mtn, Hex River Mtns, Keeromsberg Mtn (alt.: 765–2 330 m)	Koue Bokkeveld Mtns (alt.: 1 760–1 830 m)	Skurweberg, Witsenberg, Hex River Mtns (alt.: 1 330–2 000 m)	Langeberg Mtns: Montagu to Gouritz River (alt.: 300–1 330 m)	Mountains east and south of Ceres	Waboomsberg in Montagu Dist. (alt.: 1 280–1 400 m)
Flowering time	all year except June	September–February	October–January	September–December	all year	July–March	June–August
Habitat	lower mountain slopes, flats	mountain slopes	upper mountain slopes	stony or shaly mountain slopes	mountain slopes and sandy flats	summit and mountain valley	level sandy area on mountain
Flower colour	cream, cream tinged pink, pale mauve	cream, mauve, dirty violet	cream	cream, pale yellow	cream	cream	cream
Regeneration	reseeder or resprouter	reseeder	reseeder	reseeder	reseeder or resprouter	reseeder	reseeder

SPECIATION

Speciation in the Cape flora is generally thought to be allopatric (Goldblatt 1978). Goldblatt (1981) noted that the geographical component, with its accompanying edaphic and microclimatic variation is clearly the most significant factor in the evolution of the genus *Homeria*. According to Linder (1985), most of the species diversity in the Cape flora is accounted for by species replacement along ecological gradients rather than by geographical replacement patterns.

The causative agents of speciation can be inferred only from comparison of the phylogeny of a group with its ecology. A comparison of the biological differences of the species at the terminal nodes should give an indication of the factors that lead to speciation of the species pairs/triplets. The lower nodes of the cladogram are not as informative because subsequent evolution may obscure the factors that led to speciation.

In *Lachnaea* seven species pairs/triplets on the cladograms of Analyses A (Figure 15) and B (Figure 16) were analysed. The species pair *L. ericoides* and *L. stokoei* was not included, as the last-mentioned species is only known from two herbarium collections with very little information. Ecological factors taken into account in this analysis are given in Table 16, and the differences between the sister species for each pair/triplet are tabulated in Table 17.

It appears that the most likely main causative agent for speciation in *Lachnaea* is geographic isolation. Six of the seven species pairs/triplets are allopatric. Additional ecological differences between sister species are also evident in two species pairs. In species pair 6 (*L. pendula* and *L. penicillata*) allopatry and altitudinal differences characterize the sister species, whereas in species pair 4 (*L. aurea* and *L. striata*) allopatry and allochrony characterize the sister species. The species in species pair 4 differ markedly in flower colour. It is unclear whether the shift in colour followed the speciation event or whether it preceded it. Different methods of surviving fire (e.g. reseeder vs resprouter) add another variable along which diversification may have taken place (Linder 1985). Where the species of pair 1 (*L. grandiflora* and *L. uniflora*) are sympatric the regeneration strategy differs: *L. grandiflora* is a resprouter and *L. uniflora* a reseeder. It is therefore possible that the regeneration strategy could have played a role in speciation. In species pair 3 (*L. capitata* and *L. densiflora*) it is unclear what caused the speciation.

7. Taxonomic treatment

Lachnaea *L.*, Species plantarum: 560 (1753); L.:169, n. 441 (1754); Crantz: 128 (1766); Juss.: 77 (1789); Lam.: 373 (1792); Willd.: 434 (1799); C.F.Gaertn.: 195 (1807); W.T.Aiton: 415 (1811); Meisn.: 408 (1840); Meisn.: 574 (1857); Baill.: 108 (1880); Benth. & Hook.: 196 (1880); Gilg: 240 (1894); C.H.Wright: 18 (1915); Domke: 136 (1934); R.A.Dyer: 395 (1975); Bredenkamp & Beyers: 545 (2000). Lectotype species: *L. eriocephala* L. vide Domke: 136 (1934).

Cryptadenia Meisn. in Linnaea 14: 404 (1840); Meisn. : 573 (1857); Benth. & Hook.f.: 195 (1880); Gilg: 239 (1894); C.H.Wright: 15 (1915); Domke: 136 (1934); R.A.Dyer: 395 (1975). Lectotype species: *C. grandiflora* (L.f.) Meisn. (= *Lachnaea grandiflora* (L.f.) Baill.) vide Domke: 137 (1934).

Radojitskya Turcz.:176 (1852); Turcz.: 742 (1853). Type species: *R. capensis* Turcz. (= *Lachnaea axillaris* Meisn.) selected here.

Calysericos Eckl. & Zeyh. ex Meisn.: 573 (1857) nom. nud. in synonymy.

Gonophylla Eckl. & Zeyh. ex Meisn.: 574 (1857) nom. nud. in synonymy.

Pre-Linnaean: *Lachara* (?err. typogr.) Royen ex L., Systema naturae, edn 2: 22 (1740). *Lachnaea* [*Van Royen*] L.: 165, n. 382 (1742).

Erect to decumbent, slender to compact shrubs or shrublets, single-stemmed or multistemmed at base. *Branches* terete or ridged below leaf bases, glabrous or variously pubescent. *Leaves* alternate or decussate, imbricate to scattered, adpressed to patent, sessile, epistomatic or amphistomatic, glabrous or occasionally margins ciliate or with tuft of hairs at apex, linear to ovate to obovate, occasionally circular, coriaceous, occasionally slightly fleshy; adaxially ± flat to concave, usually white-punctulate; abaxially ± flat to convex, enervate, subkeeled to keeled or ribbed. *Inflorescence* a terminal capitulum, or a bracteate or ebracteate umbel, or 1-flowered. *Flowers* bisexual, subactinomorphic to strongly zygomorphic, sessile or pedicellate. *Hypanthium* with circumscissile articulation above ovary; basal portion persistent, enclosing expanding fruit and not ruptured by it, narrowly ovoid to obovoid, usually glabrous inside, glabrous or variously pubescent outside; upper portion cylindrical-obconical to widely obconical, narrowly funnel-shaped to funnel-shaped, cup-shaped, cup-shaped narrowing into a tube at base or occasionally cup-shaped with a basal invagi-

nation, glabrous or variously pubescent inside and outside. *Sepals* 4, ascending to patent, ± equal to unequal, narrowly elliptic to oblate, narrowly ovate to widely depressed-ovate or obovate to widely obovate, adaxially and abaxially variously pubescent or glabrous. *Petals* absent. *Stamens* all exserted, or outer whorl exserted and inner whorl semi-exserted or included; outer, antisepalous whorl arising on sepals, usually near base, to a $^1/_3$ down upper portion of hypanthium; inner, antipetalous whorl arising at rim to $^2/_3$ down upper portion of hypanthium, often shorter than outer whorl; anthers basifixed, introrse, ellipsoid to depressed spheroid, occasionally oblong, occasionally with broad connective tissue abaxially. *Floral scales* 8, exserted or included, arising in a single whorl below stamens and alternating with them, at various levels in upper portion of hypanthium, usually basally but occasionally abaxially attached to hypanthium, linear to oblong, narrowly obovoid to widely obovoid, or narrowly ellipsoid to subglobose, usually glabrous, translucent and white to yellow in fresh state, sometimes secretory. *Ovary* superior, sessile, narrowly ellipsoid to ellipsoid, or ovoid to obovoid, glabrous to pubescent, unilocular with a single, pendulous, anatropous ovule. *Style* lateral, basically cylindric, but ranging from filiform to narrowly obconical, glabrous to pubescent. *Stigma* penicillate and brush-like, capitate and papillate or conical and papillate. *Fruit* an achene, enclosed in persistent basal portion of hypanthium; pericarp dry, thin; seedcoat thick, crustaceous.

A genus of 40 species endemic to the Cape Floristic Region.

KEY TO SPECIES

Note: flower measurement given is hypanthium length plus sepal length.

1a Flowers solitary, terminal (may appear axillary when much reduced lateral branches comprise one pair of leaves):
2a Leaves alternate . . . . . 10. *L. ruscifolia*
2b Leaves opposite/decussate:
3a Upper portion of hypanthium funnel-shaped (stalked); floral scales exserted . . . . . 9. *L. laxa*
3b Upper portion of hypanthium not stalked, obconical or cup-shaped; floral scales included:
4a Flowers longer than 11 mm; floral scales semiterete, abaxially attached to hypanthium wall:
5a Basal portion of hypanthium covered outside with blunt hairs . . . . . 1. *L. uniflora*
5b Basal portion of hypanthium covered outside with acicular hairs . . . . . 2. *L. grandiflora*
4b Flowers shorter than 9 mm; floral scales terete, basally attached to hypanthium wall:
6a Hypanthium glabrous outside . . . . . 6. *L. axillaris*
6b Hypanthium pubescent outside:
7a Flowers dark red, borne on short branches and facing downwards . . . . . 5. *L. pudens*
7b Flowers white, cream or pink to dark pink, if borne on short branches then not facing downwards:
8a Upper portion of hypanthium cup-shaped, with or without basal invagination:
9a Stigma conical, papillate . . . . . 3. *L. filicaulis*
9b Stigma capitate, papillate . . . . . 4. *L. gracilis*
8b Upper portion of hypanthium narrowly obconical with basal invagination:
10a Basal portion of hypanthium glabrous outside; stigma conical . . . . . 7. *L. leipoldtii*
10b Upper half of basal portion of hypanthium pubescent outside, trichomes obtuse; stigma linear-conical . . . . . 8. *L. pusilla*
1b Flowers three to more than 50 in terminal capitula or umbels:
11a Inflorescence a capitulum: flowers sessile, borne on thickened floral axis:
12a Upper portion of hypanthium not stalked, obconical:
13a Capitulum globose with many open flowers at a time; upper portion of hypanthium widely obconical; sepals patent, tomentose on outside; floral scales exserted . . . . . 16. *L. densiflora*
13b Capitulum with few open flowers at a time; upper portion of hypanthium obconical; sepals ascending, sericeous on outside; floral scales included . . . . . 15. *L. capitata*
12b Upper portion of hypanthium stalked, funnel-shaped:
14a Sepals unequal, anterior sepal at least twice as long as other three:
15a Capitula pompom-like; leaves narrowly ovate to obovate, amphistomatic (± punctulate ad- and abaxially when dry) . . . . . 13. *L. filamentosa*
15b Capitula daisy-like; leaves obovate, epistomatic (± punctulate adaxially when dry) . . . . . 12. *L. macrantha*
14b Sepals equal to slightly unequal, anterior sepal never much longer than other three:
16a Capitula 25–55 mm diam.; hypanthium longer than 15 mm, narrowly funnel-shaped; epals equal; leaves amphistomatic . . . . . 14. *L. pomposa*
16b Capitula 15–25 mm diam.; hypanthium shorter than 10 mm; sepals equal to unequal; leaves epistomatic . . . . . 11. *L. alpina*
11b Inflorescence an umbel (sometimes resembling a capitulum): flowers pedicellate:
17a Umbel ebracteate:
18a Leaves alternate:
19a Leaf margin crisped-ciliate . . . . . 22. *L. striata*
19b Leaf margin glabrous or only apex with tuft of hairs:

20a Upper portion of hypanthium obconical; floral scales semiterete, abaxially attached to hypanthium wall . . . . . 21. *L. stokoei*
20b Upper portion of hypanthium funnel-shaped:
21a Leaf apex with tuft of hairs . . . . . 20. *L. ericoides*
21b Leaf apex glabrous:
22a Stigma capitate, papillate . . . . . 19. *L diosmoides*
22b Stigma brush-like:
23a Basal portion of hypanthium hairy on outside; trichomes obtuse or subacute . . . . . 17. *L. nervosa*
23b Basal portion of hypanthium usually glabrous on outside, if hairy then trichomes acicular . . . . . 18. *L. sociorum*
18b Leaves opposite:
24a Trichomes on outside of basal portion of hypanthium obtuse; sepals dorsally (outside) sericeous . . . . . 24. *L. burchellii*
24b Trichomes on outside of basal portion of hypanthium acicular; sepals dorsally (outside) tomentose . . . . . 25. *L. glomerata*
17b Umbel pseudobracteate or bracteate:
25a Sepals unequal, anterior sepal at least twice as long as posterior sepal:
26a Leaves alternate; flowers golden yellow . . . . . 23. *L. aurea*
26b Leaves opposite; flowers cream to mauve . . . . . 35. *L. eriocephala*
25b Sepals ± equal, if unequal then not as above:
27a Inflorescence pendulous . . . . . 33. *L. pendula*
27b Inflorescence erect:
28a Pedicels not elongating in fruiting stage . . . . . 26. *L. laniflora*
28b Pedicels elongating in fruiting stage:
29a Pedicels terete, not abaxially elongating beyond flower attachment:
30a Floral scales arising below midway in upper portion of hypanthium:
31a Upper portion of hypanthium funnel-shaped (Figure 8) . . . . . 31. *L. funicaulis*
31b Upper porton of hypanthium cup-shaped narrowing into a tube at base (Figure 8T, W):
32a Inflorescence pseudobracteate; flowers 3.3–5.5 mm long; outer stamen whorl exserted, inner whorl semi-exserted or included . . . . . 30. *L. greytonensis*
32b Inflorescence bracteate: flowers 7.0–9.5 mm long; both stamen whorls exserted . . . . . 32. *L. oliverorum*
30b Floral scales arising in mouth of hypanthium:
33a Antesepalous stamens arising in lower third of sepals . . . . . 29. *L. marlothii*
33b Antesepalous stamens arising at base of sepals:
34a Upper portion of hypanthium and sepals villous-tomentose outside . . . . . 28. *L. villosa*
34b Upper portion of hypanthium and sepals sericeous outside:
35a Umbel pseudobracteate, with up to four open flowers at a time; style glabrous . . . . . 27. *L. elsieae*
35b Umbel bracteate, with one open flower at a time; style covered in upper half with silky ascending hairs . . . . . 34. *L. penicillata*
29b Pedicels dorsoventrally flattened, abaxially elongating beyond point of flower attachment:
36a Leaves glaucous, navicular (boat-shaped) . . . . . 36. *L naviculifolia*
36b Leaves not as above:
37a Involucral bracts or bract-like leaves ciliate:
38a Low, straggling shrublet up to 0.2 m tall; umbel pseudobracteate, with 3–5 open flowers at a time . . . . . 37. *L. rupestris*
38b Slender, erect shrub up to 0.6(–0.9) m tall; umbel bracteate, with up to 14 open flowers at a time . . . . . 38. *L. globulifera*
37b Involucral bracts or bract-like leaves eciliate :
39a Pedicels linear in outline, villous; flowers 10.5–25.0 mm long . . . . . 39. *L. montana*
39b Pedicels narrowly obovate to obovate in outline, adaxially sericeous, abaxially villous, apex usually emarginate; flowers 5.1–8.2 mm long . . . . . 40. *L. pedicellata*

1. **Lachnaea uniflora** *(L.) Crantz*, Institutiones rei herbariae 1: 130 (1766); Beyers: 45 (1997). Syntypes: Burm., Rariorum africanarum plantarum: 131, t. 48, f. 1 (1739), lecto.!, here designated; Burm., Rariorum africanarum plantarum: 131 ('132'), t. 48, f. 2 (1739), this figure may represent *L. grandiflora* (L.f.) Baill.

Passerina uniflora L.: 560 (1753); P.J.Bergius: 128 (1767) pro parte; Thunb.: 75 (1794); Poir.: 42 (1804) pro parte; ? Poir: t. 291, f. 1 (1804) [illustration could be narrow-leaved form of *L. grandiflora*]; Wikstr.: 344 (1818); Thunb.: 376 (1823); Spreng.: 239 (1825). *Cryptadenia uniflora* (L.) Meisn.: 406 (1840); Hook.: 71, t. 4143 (1845); Meisn.: 573 (1857); C.H.Wright: 22 (1915).

Passerina uniflora var. *purpurea* P.J.Bergius: 128 (1767); Poir.: 42 (1804). *Passerina uniflora* var. *angustifolia* Burm.f.: 12 (1768). Type: *Thymelaea ramosa, linearibus foliis angustis, flore solitario* Burm., Rariorum africanarum plantarum: 131, t. 48, f. 1 (1739).

Note: two specimens in. LINN: *504.8* and *504.9*, are not original material. *LINN 504.8* lacks the correct corresponding *Species plantarum* number (4 in this case) which is the requisite proof that it was in Linnaeus' possession in 1753. It is therefore considered a post-1753 addition to the Linnaean herbaria and is therefore not eligible for lectotypification. Similarly *LINN 504.9* could not have formed the basis of the name as it is not even annotated by Linnaeus but by his son and is regarded as a 1772 specimen. The only available original elements therefore are the two Burman plates: fig. 1 on plate 48 with an illustra-

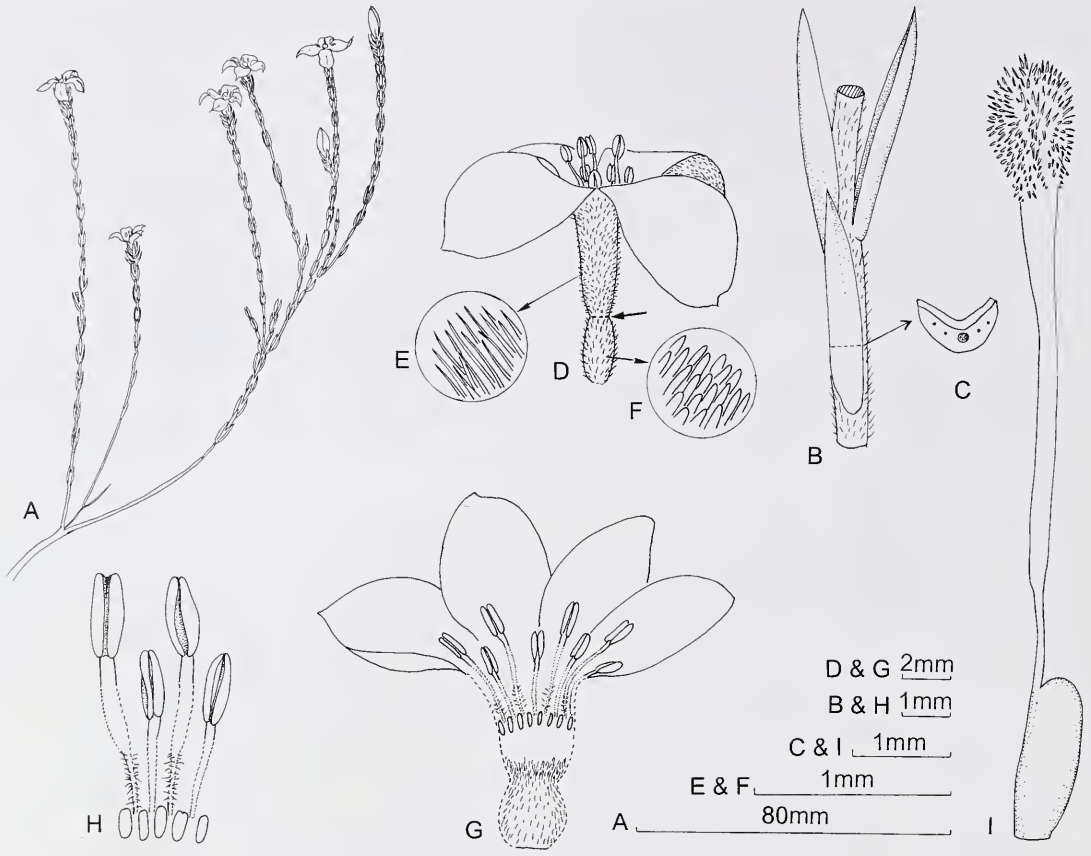

FIGURE 17.—*Lachnaea uniflora*, *Beyers 136* (NBG). A, portion of plant; B, branch with leaves; C, c/s leaf. E, F, hypanthium: E, acicular trichomes on upper portion; F, obtuse trichomes on basal portion. D, circumscission zone arrowed; G, flower with gynoecium removed; H, stamens and scales; I, gynoecium. Scale bars: A, 80 mm; B, C, E, F, H, I, 1 mm; D, G, 2 mm.

tion of the complete plant, is chosen as the lectotype since there can be no question of its identity. The other plate, t. 48, f. 2, is somewhat ambiguous, illustrating only a piece of the upper portion of the plant with broader leaves, which appears to be better matched with the species concept of *L. grandiflora*.

Erect, lax, moderately branched shrub up to 0.45 m tall, single-stemmed at base when a reseeder, or multi-stemmed at base when a resprouter. *Branches* ascending, slender, flexuose, internodes half to as long as leaves, ridged below leaf bases, glabrous or sparsely adpressed hairy, occasionally sericeous, leafy, later becoming glabrous and naked with prominent leaf scars. *Leaves* decussate, distal 2 pairs subverticillate, adpressed to ascending, scattered, sessile, epistomatic, narrowly elliptic or lanceolate, 3.3–6.7(–12.0) × 0.6–1.0 mm, coriaceous, glabrous; adaxially concave, enervate, dull, ± white-punctate; abaxially convex, subkeeled or only subkeeled in upper half, glossy, smooth or faintly nervate; apex acute to acuminate; base obtuse or rounded; margin membranous, narrow. *Inflorescence* terminal, 1-flowered, villous at floral articulation. *Flowers* sessile, subactinomorphic, pink to pinkish mauve, occasionally white, unscented. *Hypanthium* 6.8–12.0 mm long, circumscissile a $^1/_4$–$^1/_3$ from base; upper portion narrowly obconical to obconical, outside sericeous or sericeous-villose, trichomes acicular, inside densely hairy to sparsely hairy below floral scales, hirtellous on prominent ridges formed by adnate filaments of antesepalous stamens, in vicinity of floral scales glabrous; basal portion narrowly ellipsoid to ellipsoid, narrowly oblong or obovoid, outside sericeous, trichomes broad, obtuse or acute, twice as broad as those above circumscission zone, inside adpressed hairy to glabrescent. *Sepals* spreading, subequal (2 inner ones slightly smaller than outer 2), elliptic, ovate or occasionally narrowly ovate, 5.0–9.5 × 3.0–5.5 mm, apex subacute or rounded, abaxially sericeous, adaxially glabrous or occasionally sparsely adpressed hairy at apex. *Stamens* with outer, antesepalous whorl adnate to upper portion of hypanthium and becoming free at rim to $^1/_6$ way down hypanthium, exserted or semi-exserted; inner, antipetalous whorl adnate to upper hypanthium and becoming free a $^1/_5$–$^1/_3$ down hypanthium, semi-exserted or included; filaments 0.3–1.5 mm long; anthers ellipsoid, 0.8–1.5 mm long, abaxially without broad connective tissue. *Floral scales* included, arising $^1/_4$–$^1/_2$ up from circumscission zone on upper portion of hypanthium, 0.2–0.8 mm long, semiterete, abaxially adnate to hypanthium, narrowly

elliptic or oblong in outline, glabrous. *Ovary* narrowly ellipsoid to ellipsoid, 1.2–2.0 mm long, glabrous. *Style* terete-obconical, 4.5–9.8 mm long, glabrous. *Stigma* narrowly conical, narrowly ellipsoid to ellipsoid or occasionally subcapitate, elongate-papillate (Figure 17).

Distribution, ecology and variation

Lachnaea uniflora has been recorded from Darling southwards to the Peninsula and as far east as Somerset West, and inland from Twenty-four River Mountains southeast to Wolseley and the mountains around Franschhoek, at altitudes from sea level to 860 m (Figure 18).

Two distinct entities based on their mode of regeneration can be distinguished. Form A is a reseeder, growing in sandy flats from Darling to the Peninsula and eastwards to Somerset West at altitudes below 300 m. Form B, on the other hand, is a resprouter occurring further inland, at altitudes between 300 and 860 m, favouring sandy to sandy, stony soil. Numerous collections, old and recent, have been recorded from the Franschhoek area, whereas Drège's collection from Twenty-four Rivers Mountains and Schlechter's collection from Ceres Road (Wolseley) are single collections from the respective areas, collected in the nineteeth century. *Flowering time*: July to March.

Conservation status: Vulnerable (VU A1c). Most of the populations on the sandy flats north of the Cape Peninsula and on the Cape Peninsula in the vicinity of Wynberg and Constantia have disappeared.

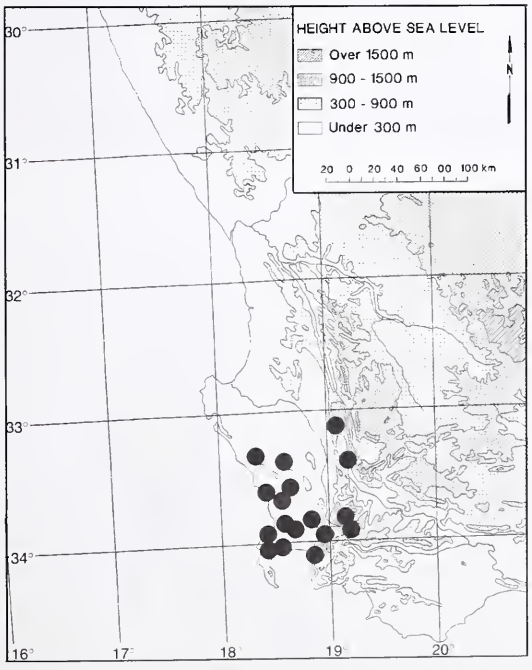

FIGURE 18.—Known distribution of *Lachnaea uniflora*.

Diagnostic characters and relationships

Lachnaea uniflora is closely related to *L. grandiflora*, both having similar, large, solitary flowers, but it differs from the latter in having obtuse trichomes on the lower portion of the hypanthium and acute ones on the upper portion. In *L. grandiflora* the trichomes are acute on both portions on the outside of the hypanthium. The reseeding form of *L. uniflora* is sympatric with *L. grandiflora* but can easily be distinguished from the latter, which is a resprouter. The resprouting form of *L. uniflora* appears to be allopatric with *L. grandiflora*.

Vouchers: *Beyers 136* (BOL, K, MO, NBG, PRE, S), *269* (K, NBG, PRE); *Boucher 4570* (NBG, PRE); *Esterhuysen 16015* (BOL); *Rourke 725* (NBG); *Zeyher 1485* (BOL, GRA, PRE, SAM, K). Total number of specimens examined: 138.

2. **Lachnaea grandiflora** *(L.f.) Baill.*, The natural history of plants 6: 109, t. 77 (1880); Beyers: 45 (1997). Type: *LINN 504.13* (LINN, lecto., here designated; –NBG, photocopy!).

Passerina grandiflora L.f.: 226 (1782); Curtis: t. 292 (1795); Willd.: 432 (1799), excluding synonym *P. linoides* Thunb.; Poir.: 44 (1804); Wikstr.: 345 (1818). *Cryptadenia grandiflora* (L.f.) Meisn.: 405 (1840); Meisn.: 552 (1843); Meisn.: 573 (1857); Gilg: 234, t. 83E, 240 (1894); C.H.Wright: 16 (1915); Levyns: 601 (1950).

Passerina uniflora L. var. *alba* P.J. Bergius: 129 (1767); Poir.: 42 (1804). Type: Burm., Rariorum africanarum plantarum:123, t. 46, f. 1 (1739) (lecto.!, here designated).

Note: Bergius (1767) also refers to Herm. Afr. 23 in the protologue. This is only a literature reference as no specimen was found in Vol. 4-1 (Burman 1737) which does contain some South African material, matching the Hermann polynomial as cited by Bergius (S. Cafferty pers. comm.). According to Cafferty: 'Herm. afr.' refers to an appendix by Paul Hermann, Cat. Pl. Afr., in Burman's *Thesaurus zeylanicus* (1737), where the cited polynomial is listed on page 23.

? *Passerina uniflora* L. var. *latifolia* Burm.f.:12 (1768). Type: Burm., Rariorum africanarum plantarum: 131, t. 48, f. 2 (1739) (icono.!).

Cryptadenia breviflora Meisn.: 406 (1840); Meisn. 14: 573 (1857); C.H.Wright: 17 (1915). Syntypes: in single, sandy island in Berg River, alt. 400 ft, (III. E. b), *Drège s.n.* (not yet located); Table Mountain, *Ecklon 369* (S, lecto.! here designated; K!, NBG!, PRE!, isolecto.).

Note: unfortunately the sheet from Meisner's Herbarium (NY) with notes written by him comprises two different collections of Ecklon without stating the collection number. The sheet from S is chosen as the lectotype because Meisner communicated with Sonder, as stated on the sheet in NY, and this specimen is most likely from Sonder's Herbarium, which is now incorporated in S.

Passerina campanulata E.Mey. ex Meisn.: 407 (1840) nom. nud. in synonomy.

? *P. uniflora* sensu Meisn.: 407 (1840). Syntypes: Herb. Lam. ex parte (not seen); Burm., Rariorum africanarum plantarum t. 48, f. 2 (1739), ? non L.

Calysericos canaliculata Eckl. & Zeyh. ex Drège: 210 (1847b) nom. nud. in synonymy.

Calysericos grandiflora Eckl. & Zeyh. ex Meisn.: 573 (1857) nom. nud. in synonymy.

Calysericos parviflora Eckl. & Zeyh. ex Meisn.: 574 (1857) nom. nud. in synonymy.

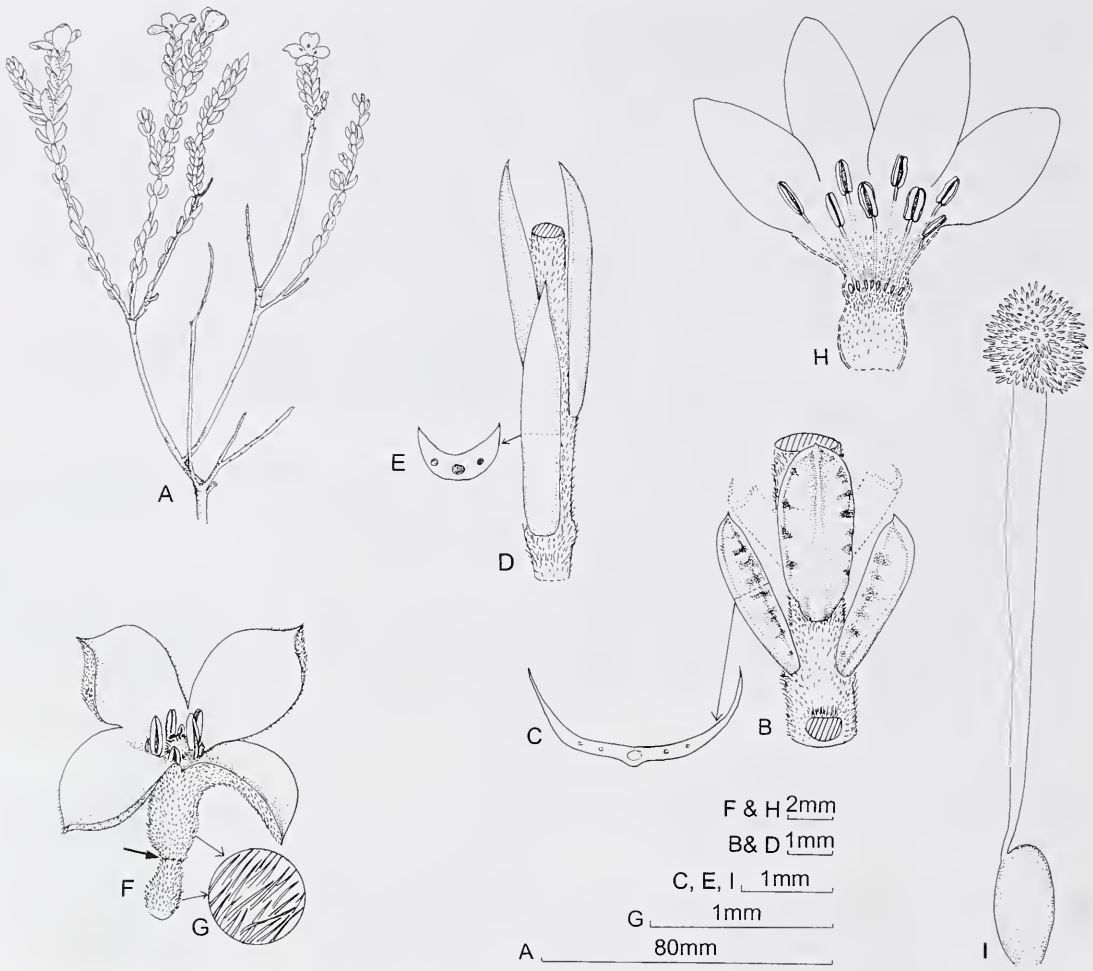

FIGURE 19.—*Lachnaea grandiflora*. A, portion of plant; B, D, branches with leaves; C, E, c/s leaves. F, H, flower: F, circumscission zone arrowed; H, l/s with gynoecium removed. G, acicular trichomes on hypanthium; I, gynoecium. A–C, F–I, *Beyers 129* (NBG); D, E, *Hansford 86* (NBG). Scale bars: A, 80 mm; B–E, G, I, 1 mm; F, H, 2 mm.

Calysericos subulata Eckl. & Zeyh. ex Meisn.: 574 (1857) nom. nud. in synonymy.

Calysericos tabularis Eckl. & Zeyh. ex Meisn.: 574 (1857) nom. nud. in synonymy.

Cryptadenia grandiflora (L.f.) Meisn. var. *latifolia* Meisn.: 573 (1857); C.H.Wright: 16 (1915). Type: specimen without collector and locality in herb. DC [possibly in G-DC], fide Meisner (not seen).

Erect or occasionally straggling, moderately to much-branched shrub 0.2–0.6(–1.0) m tall, multistemmed at base; resprouter. *Branches* ascending to decumbent, slender to moderately thick, flexuose to semi-rigid, internodes $^1/_4$–$1^1/_2$ length of leaves, ridged below leaf bases, usually adpressed-puberulent, occasionally sparsely hairy, leafy, later glabrescent and naked with prominent leaf scars. *Leaves* decussate with distal 2 pairs subverticillate, subadpressed to ascending, ± imbricate or scattered, sessile, epistomatic, narrowly elliptic to elliptic, narrowly ovate or narrowly obovate, 2.2–11.5 × 0.8–3.0 mm, coriaceous, glabrous; adaxially obtusely concave or concave, enervate or faintly mid-veined, dull, ± white-punctate; abaxially convex, occasionally nervate, subkeeled or only subkeeled in upper half, glossy, smooth to rugose, sometimes upper leaves below inflorescence with a reddish brown tinge; apex acute, mucronulate or mucronate; base obtuse or rounded; margin membranous, narrow to broad, when broad usually conspicuously corrugated (with transverse folds). *Inflorescence* terminal, 1-flowered. *Flowers* sessile, subactinomorphic, creamy white, white with a pink tinge, pinkish mauve or pink, unscented. *Hypanthium* 5–14 mm long, circumscissile $^1/_5$–$^1/_3$ from base; upper portion narrowly obconical to obconical; basal portion narrowly ellipsoid to ellipsoid, occasionally widely obovoid, sericeous outside, trichomes of base and upper portion acicular, upper portion adpressed hairy inside from floral scales downwards, glabrous or sparsely hairy above; basal portion adpressed hairy inside in upper $^1/_3$–$^1/_2$, glabrous below. *Sepals* ascending to spreading, subequal (2 inner

ones slightly smaller than outer 2), elliptic, obovate or occasionally ovate, 5.2–14.5 × 3–8 mm, apex subacute to obtuse, abaxially sericeous, adaxially usually glabrous, occasionally glabrescent. *Stamens* of outer, antesepalous whorl exserted, adnate to upper portion of hypanthium and becoming free at base to $^1/_5$ way up sepals; inner, antepetalous whorl semi-exserted or included, occasionally exserted, adnate to upper hypanthium and becoming free at rim to a $^1/_3$-way down hypanthium; filaments 0.3–2.2 mm long; anthers narrowly ellipsoid to ellipsoid, 1.0–2.6 mm long, abaxially without broad connective tissue. *Floral scales* enclosed, arising $^1/_6$–$^1/_3$ way, occasionally $^1/_2$ way up from circumscission zone on upper portion of hypanthium, semiterete, abaxially adnate to hypanthium, narrowly elliptic or oblong in outline, 0.4–1.2 mm long, glabrous, yellow in fresh state. *Ovary* ellipsoid, 1.0–2.2 mm long, glabrous. *Style* terete-obconical, 5.2–11.5 mm long, glabrous, occasionally glabrescent. *Stigma* capitate, elongate-papillate (Figure 19).

Distribution, ecology and variation

Lachnaea grandiflora occurs on sandy flats and sandy areas on lower mountain slopes from Swartboskraal in the Clanwilliam District south and southeast to the Cape Peninsula, Citrusdal, Tulbagh, Worcester and Bredasdorp, at altitudes between 15 and 1 000 m (Figure 20). One isolated record from 3322 (Oudtshoorn): Buffelsberg (–DC) in the Kammanassie Mountains in the Little Karoo, at altitude of 1 660 m, (*Viviers & Vlok 30* NBG), appears out of place and needs to be investigated. This sheet could possibly have an incorrect label.

Two intergrading morphs, based on the leaves, can be discerned in this species. Form A with leaves narrowly elliptic to elliptic, narrowly ovate or narrowly obovate, abaxially usually rugose and with a broad membranous margin with transverse corrugations, or at least the distal two pairs of leaves below the inflorescence with broad, membranous, corrugated margins. In form B the leaves

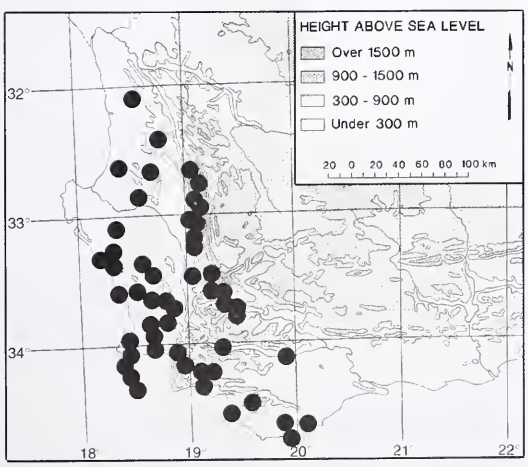

FIGURE 20.—Known distribution of *Lachnaea grandiflora*.

are narrowly ovate to narrowly obovate, sometimes almost linear-elliptic, with a very narrow, smooth membranous margin. Form A occurs predominantly from Malmesbury to the Cape Peninsula and eastwards to Houhoek. In the Bredasdorp area the leaves of at least the distal two leaf pairs below the inflorescence have broad membranous margins which are either smooth or faintly corrugated. Form B occurs from Swartboskraal in the Clanwilliam District in the north, southeast through Citrusdal to Worcester. The narrow-leaved form appears to occur in drier conditions. Between these two forms there is a continuum of variation with regard to the width of the membranous margin and the surface of the leaves, which makes a reliable subdivision of this species impossible. *Flowering time*: all months except July.

Conservation status: Vulnerable (VU A1c). Most of the populations on sandy flats have disappeared.

Diagnostic characters and relationships

Lachnaea grandiflora is closely related to *L. uniflora*. Their inflorescence and floral structure are similar. The narrow-leaved form of *L. grandiflora* has in the past been confused with *L. uniflora*. *L. grandiflora* is multistemmed at the base, resprouting after fires, whereas in *L. uniflora* two distinct forms have been identified, namely a single-stemmed reseeder and a multistemmed resprouter. Although the hypanthium of both species is sericeous on the outside, the trichomes of the basal portion of the hypanthium in *L. uniflora* are blunt (obtuse), whereas those in *L. grandiflora* are acicular, similar to those on the upper hypanthium.

Vouchers: *Beyers 151* (NBG, PRE), *168* (K, NBG, PRE), *196* (NBG), *242* (BOL, K, MO, NBG, NY, PRE, S, Z), *250* (BOL, K, NBG, PRE); *Boucher 3622* (NBG, PRE); *Compton 18923* (NBG); *Oliver 5479* (NBG, PRE); *Vlok 2179* (K, NBG, PRE, S). Total number of specimens examined: 251.

3. **Lachnaea filicaulis** *(Meisn.) Beyers* in Bothalia 27: 45 (1997). Type: Cape, locality unknown, *Drège 7367* (NY, holo.!–fragment in capsule on *Burchell 7540*; P!, iso.).

Cryptadenia filicaulis Meisn.: 407 (1840); Drège: 210 (1847b); Meisn.: 574 (1857); C.H.Wright: 17 (1915).

Gnidia genistifolia Eckl. & Zeyh. ex Meisn.: 574 (1857) nom. nud. in synonymy.

Erect, moderately branched shrub up to 0.4 m tall, multistemmed at base; resprouter. *Branches* erect to flexuous, slender, ridged below leaf bases, sericeous, leafy, becoming sparsely hairy and naked without prominent leaf scars. *Leaves* decussate, with distal 2 pairs of leaves usually subverticillate, ascending to patent, imbricate to distant, sessile, epistomatic, lanceolate, 3.6–8.0(–12.0) × 0.6–1.0(–1.5) mm, coriaceous, glabrous; adaxially concave to obtusely concave, smooth, dull, ± white-punctate; abaxially convex, glossy, smooth; apex mucronate or acuminate; base obtuse. *Inflorescence* terminal, 1-flowered, but appearing to be axillary when much reduced, lateral branches comprise only 1 pair of leaves

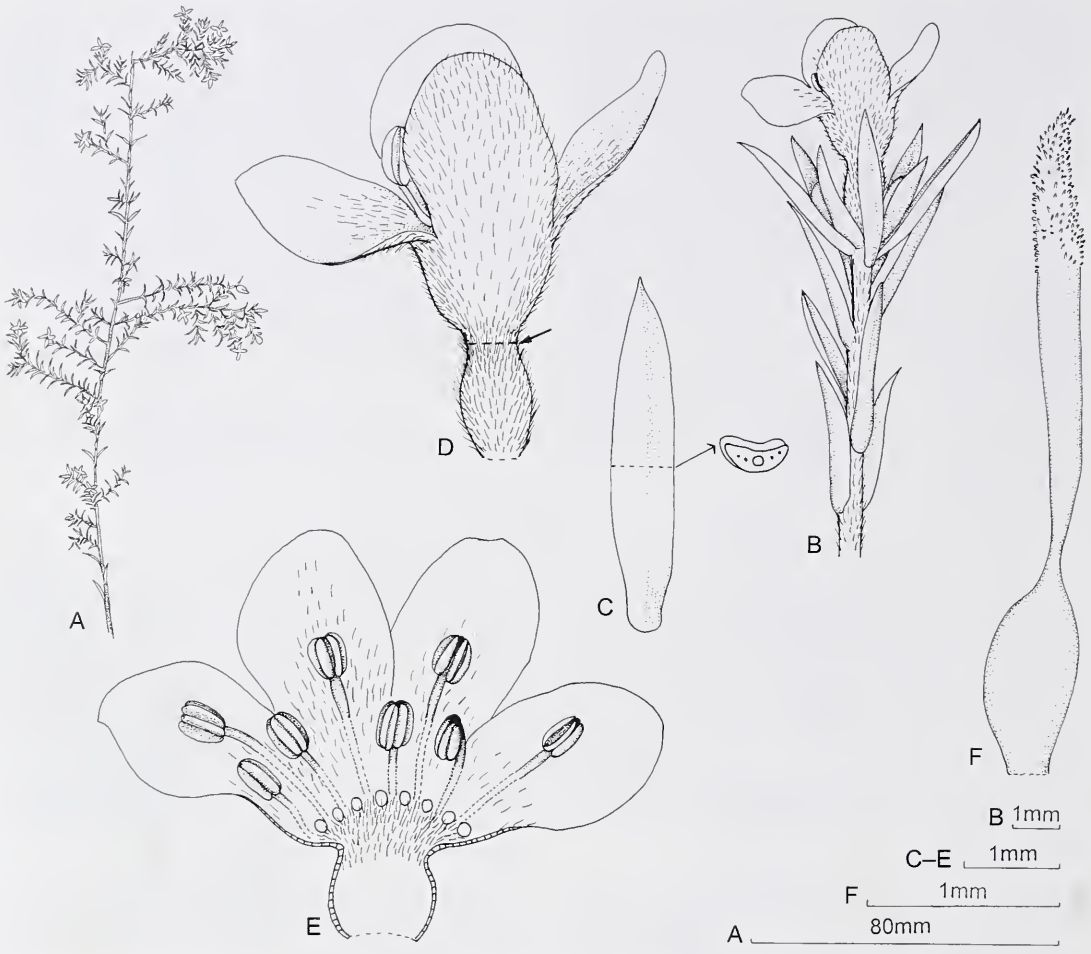

FIGURE 21.—*Lachnaea filicaulis*, *McDonald 1988* (NBG). A, portion of plant; B, flowering branch; C, leaf, abaxial view and c/s. D, E, flower: D, circumscission zone arrowed; E, l/s with gynoecium removed. F, gynoecium. Scale bars: A, 80 mm; B–F, 1 mm.

and 1 flower, densely sericeous at floral articulation. *Flowers* sessile, subactinomorphic, cream or pink. *Hypanthium* 3.0–4.5 mm long, circumscissile $^1/_3$–$^2/_3$ from base; upper portion cup-shaped; basal portion narrowly ellipsoid to ellipsoid or narrowly ovoid to ovoid, sericeous outside; upper portion adpressed-puberulent inside but barbate above circumscission zone in vicinity of floral scales; basal portion glabrous inside. *Sepals* ascending, subequal, elliptic, ovate, obovate to subrotund, 1.3–3.0 × 1.2–2.0 mm, obtuse, abaxially sericeous, adaxially puberulent to glabrescent. *Stamens* exserted or only outer, antesepalous whorl exserted and inner, antipetalous whorl semi-exserted; antesepalous whorl arising usually at rim but occasionally $^1/_3$ way down upper portion of hypanthium, inner, antepetalous whorl arising $^1/_3$–$^1/_2$ down upper portion of hypanthium; filaments 0.3–0.9 mm long; anthers widely oblong to widely ellipsoid, 0.5–1.0 mm long, abaxially with broad connective tissue. *Floral scales* arising just above circumscission zone immediately below antepetalous stamens, subrotund, 0.3–0.5 mm long, glabrous. *Ovary* ellipsoid, ovoid or obovoid, 1.0–1.6 mm long, usually glabrous but occasionally adpressed hairy near apex. *Style* terete-obconical, 1.4–2.8 mm long, glabrous. *Stigma* conical and papillate (Figure 21).

Distribution and ecology

Lachnaea filicaulis occurs on the flats and lower mountain slopes in the southwestern and southern part of Western Cape from the Palmiet River in the Caledon District eastwards to Riversdale at altitudes below 365 m (Figure 22). *Flowering time*: August to June.

Conservation status: Vulnerable (VU A1ce). The habitat of this species has been restricted through the effects of human activities and invasion by alien invader plants.

Diagnostic characters and relatonships

Lachnaea filicaulis is distinguished from *L. axillaris* by the upper portion of the hypanthium being cup-

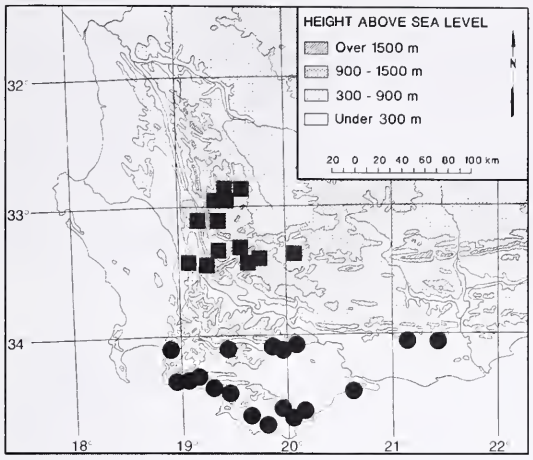

FIGURE 22.—Known distribution of *Lachnaea filicaulis*, ●; and *L. gracilis*, ■.

shaped without a basal invagination, the hypanthium and sepals being sericeous on the outside, and by the conical, papillate stigma.

Vouchers: *Dahlgren & Peterson 487* (NBG); *De Vos 1120* (NBG, PRE); *Esterhuysen 34370* (BOL, PRE, S); *McDonald 1989* (K, NBG, PRE); *Oliver 9803* (K, NBG, PRE); *Schlechter 1906* (BOL, GRA, Z). Total number of specimens examined: 56.

4. **Lachnaea gracilis** *Meisn.* in Linnaea 14: 421 (1840); Drège: 114 (1843); Meisn.: 579 (1857). Type: Hexrivier, alt. 1000–1500 ft (IV. A), *Drège s.n.* [*583*] (NY, holo.!; P!, iso.).

Erect, lax, moderately branched shrub up to 2 m tall, single-stemmed and branching at base, when grazed tends to have low, compact, decumbent habit; reseeder. *Branches* erect to flexuous, slender, internodes $^1/_2$–$^1/_4$ as long as leaves, subridged or ridged below leaf bases, sparsely adpressed hairy, leafy, becoming glabrous and naked without prominent leaf scars. *Leaves* decussate, with distal 2 pairs usually subverticillate, adpressed to ascending, distant, sessile, epistomatic, narrowly elliptic to elliptic or narrowly obovate to obovate, (3.1–)3.5–8.3 × 0.8–1.5(–3.0) mm, coriaceous, glabrous; adaxially flat or obtusely concave, smooth, dull, ± white-punctate; abaxially flat or obtusely convex, occasionally subkeeled at apex, glossy or glaucous, smooth; apex acute, acuminate or obtuse; base obtuse. *Inflorescence* terminal, 1-flowered, but may appear axillary when much reduced, lateral branches comprise only 1 pair of leaves and a solitary flower, sericeous at floral articulation. *Flowers* sessile, subactinomorphic, cream usually turning pink with age. *Hypanthium* 2.4–5.0 mm long, circumscissile $^1/_2$–$^3/_4$ way from base; upper portion cup-shaped occasionally with a basal invagination; basal portion narrowly ellipsoid to ellipsoid or narrowly ovoid to ovoid, sericeous outside, upper portion adpressed-puberulent or glabrous inside but barbate above circumscission zone in vicinity of floral scales; basal portion glabrous inside, but sometimes adpressed-puberulent towards circumscission zone. *Sepals* patent, subequal, ovate to widely ovate, or orbicular to oblate, 1.5–3.0 × 1.5–2.6 mm, obtuse or rounded, abaxially sericeous, adaxially adpressed-puberulent or glabrous. *Stamens* exserted or outer, antesepalous whorl exserted and inner, antepetalous whorl subexserted or included; antesepalous whorl arising at base of sepals, at rim of hypanthium or occasionally $^1/_3$ way down upper portion of hypanthium; antepetalous whorl arising $^1/_3$–$^2/_3$ down upper portion of hypanthium; filaments 0.3–0.9 mm long; anthers widely ellipsoid to depressed spheroid, 0.6–0.9 mm long, abaxially with broad connective tissue. *Floral scales* arising just above circumscission zone immediately below antepetalous stamens, subrotund, 0.3–0.6 mm long, glabrous, yellow in fresh state. *Ovary* narrowly ellipsoid, ovoid or obovoid, 0.9–2.8 mm long, glabrous. *Style* terete-obconical, 1.3–2.8 mm long, glabrous. *Stigma* capitate and papillate (Figure 23).

Distribution and ecology

Occurs on sandy flats and mountain slopes in the Ceres, Tulbagh and Worcester Districts at altitudes between 330 and 1 660 m (Figure 22). *Flowering time*: May, July to January.

The leaf width of this taxon is variable. There is a gradation from narrowly elliptic or narrowly obovate to elliptic or obovate leaves.The leaves of those from the Katbakkies Pass area in the Ceres District and from Touws River are the broadest. With only one such variable, subspecific delimitation has not been considered.

Conservation status: Lower Risk Least Concern (LRlc). Since this species is a reseeder, it could become threatened through frequent mountain fires.

Diagnostic characters and relationships

Lachnaea gracilis is distinguished from *L. axillaris* by the hypanthium and sepals being sericeous on the outside and from *L. filicaulis* by the capitate, papillate stigma.

Vouchers: *Bean & Viviers 2613* (BOL, NBG, PRE); *Beyers 219* (K, MO, NBG, PRE, S), *254* (K, MO, NBG, PRE, S); *Bolus 13181* (BOL, PRE, S); *Marloth 3224* (BOL, NBG, PRE); *Oliver 10415* (K, MO, NBG, NY, PRE, S, Z); *Taylor 5858* (NBG). Total number of specimens examined: 89.

5. **Lachnaea pudens** *Beyers* in Beyers & A.E. van Wyk in South African Journal of Botany 64: 66 (1998a). Type: Western Cape, 3319 (Worcester): Riviersonderend Mountains, Jonaskop, upper north slopes, (–DC), *Beyers 161* (NBG, holo.!; BOL!, K!, NY!, PRE!, iso.).

Erect to decumbent, much-branched shrub up to 0.6 m tall, single-stemmed at base, branching close to ground; reseeder. *Branches* flexuous, intertwined, moderately thick, ridged below leaf bases, tomentose or tomentose-sericeous, leafy, becoming sparsely hairy and naked with prominent leaf scars; flowering branches

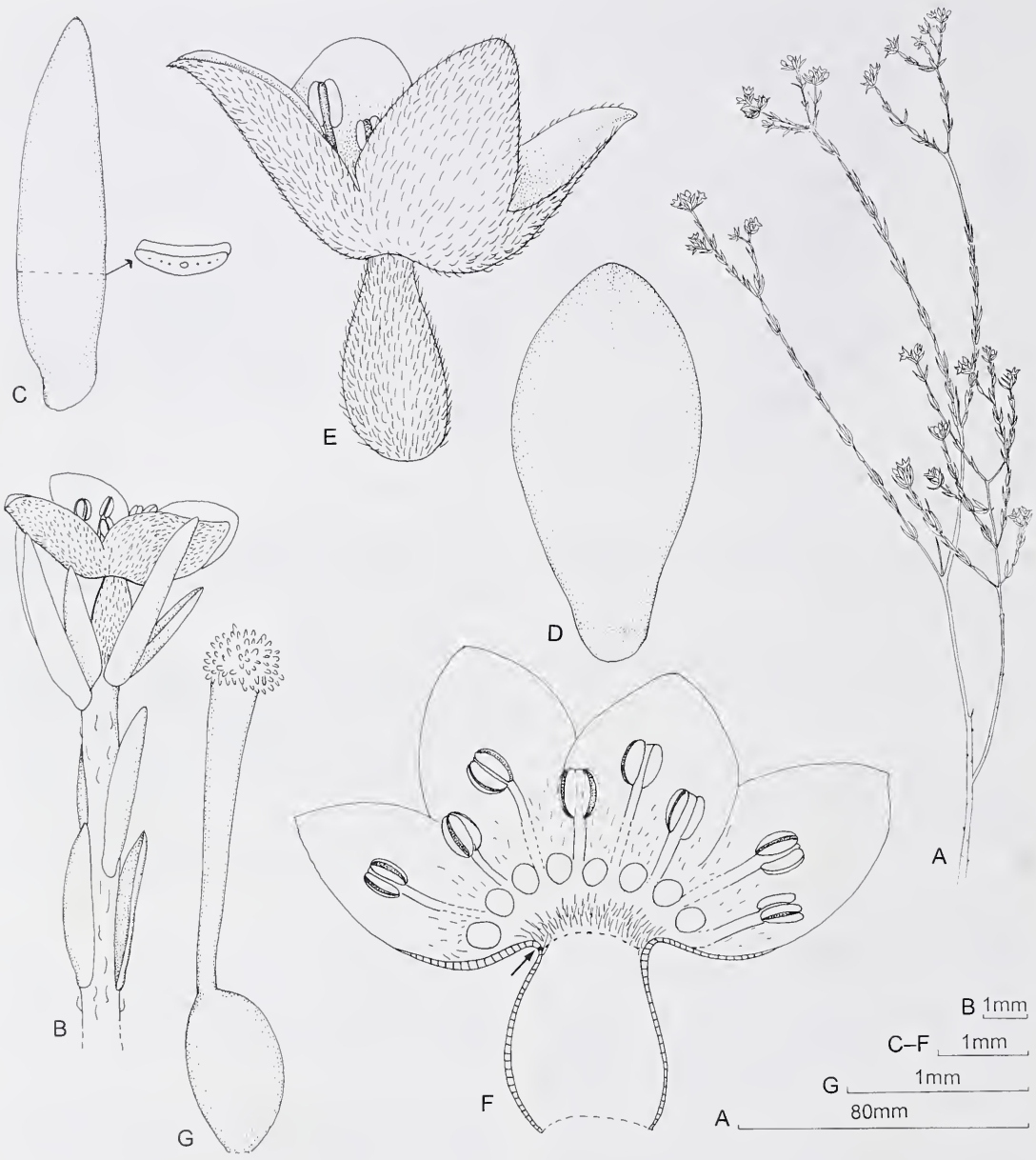

FIGURE 23.—*Lachnaea gracilis*. A, portion of plant; B, flowering branch; C, D, leaves: C, abaxial view and c/s; D, abaxial view. E, F, flower: F, l/s with gynoecium removed and circumscission zone arrowed. G, gynoecium. B, C, E–G, *Beyers 254* (NBG); D, *Bean & Viviers 2613* (NBG). Scale bars: A, 80 mm; B–G, 1 mm.

declinate. *Leaves* decussate, ascending-incurved, imbricate, distal 2 pairs of leaves inclined, erect or slightly recurved, subverticillate, sessile, elliptic, 3.8–5.7 × 1.0–1.3 mm, subfleshy, glabrous; adaxially flat to obtusely concave, smooth, dull, ± white-punctate; abaxially convex, keeled, glossy, smooth, sometimes with a reddish brown tinge; apex apiculate; base obtuse. *Inflorescence* terminal, 1-flowered, but appearing to be axillary when much reduced, lateral branches comprising only 1 pair of leaves and a solitary flower. *Flowers* sessile, subactinomorphic, dark red. *Hypanthium* 3.0–4.5 mm long, circumscissile $^{4}/_{5}$ from base; upper portion widely cup-shaped with a basal invagination; basal portion pyriform, sericeous outside; upper portion glabrous inside but villous above circumscission zone in vicinity of floral scales; basal portion sparsely hairy inside. *Sepals* patent, subequal, widely ovate or widely depressed-ovate, 2.0–3.9 × 2.6–3.6 mm, acute or obtuse, abaxially sericeous, adaxially glabrous. *Stamens* exserted, outer, antesepalous whorl adnate to upper portion of

hypanthium and becoming free just above base of sepals, inner antepetalous whorl adnate to upper hypanthium and becoming free $^2/_3$ up hypanthium; filaments 0.3–0.5 mm long; anthers depressed-spheroid, 0.5–0.6 mm long, abaxially with broad connective tissue. *Floral scales* arising midway on upper portion of hypanthium below antepetalous stamens, subrotund, 0.3–0.4 mm long, glabrous. *Ovary* ovoid, 1.0–1.3 mm long, glabrous. *Style* terete-obconical, 2.2–2.6 mm long, glabrous. *Stigma* brush-like (Figure 24).

Distribution and ecology

Lachnaea pudens occurs on the mountain slopes of Jonaskop near Villiersdorp and on the Riviersonderend Mountains above Greyton and Genadendal, at altitudes between 330 and 1 530 m, growing in sandy, stony soils overlying sandstone (Figure 25). *Flowering time*: February, May, August, October to December.

Conservation status: Vulnerable (VU D2). This species has a restricted distribution and being a reseeder, is vulnerable to frequent mountain fires.

Diagnostic characters and relationships

Lachnaea pudens is easily distinguished by the terminal, solitary, dark red flowers borne on short branches facing downwards. The floral structure is similar to that of *L. axillaris* Meisn., with the upper portion of the hypanthium cup-shaped and basely invaginated, but the flowers are sericeous on the outside, whereas in *L. axillaris* they are glabrous and cream to dark pink.

Vouchers: *Bean & Viviers 2737* (BOL, K, NBG, PRE); *Beyers 166* (BOL, K, MO, NBG, NY, PRE), *210* (BOL, K, MO, NBG, NY, PRE); *Goldblatt 4728* (NBG); *Vlok 249* (NBG). Total number of specimens examined: 41.

6. **Lachnaea axillaris** *Meisn.* in Linnaea 14: 422 (1840); Meisn.: 552 (1843); Meisn.: 578 (1857); C.H.Wright: 26 (1915). Type: Cape, locality unknown, *Drège 7371* (NY, holo.!–fragment in capsule on *Krauss 1265*; P!, iso.).

Lachnaea micrantha Schltr.: 451 (1898); C.H.Wright: 26 (1915). Type: Western Cape, on sandy hill at Elim, 300 ft. 24 April 1896, *Schlechter 7702* (Z, holo.!; BOL!, iso.).

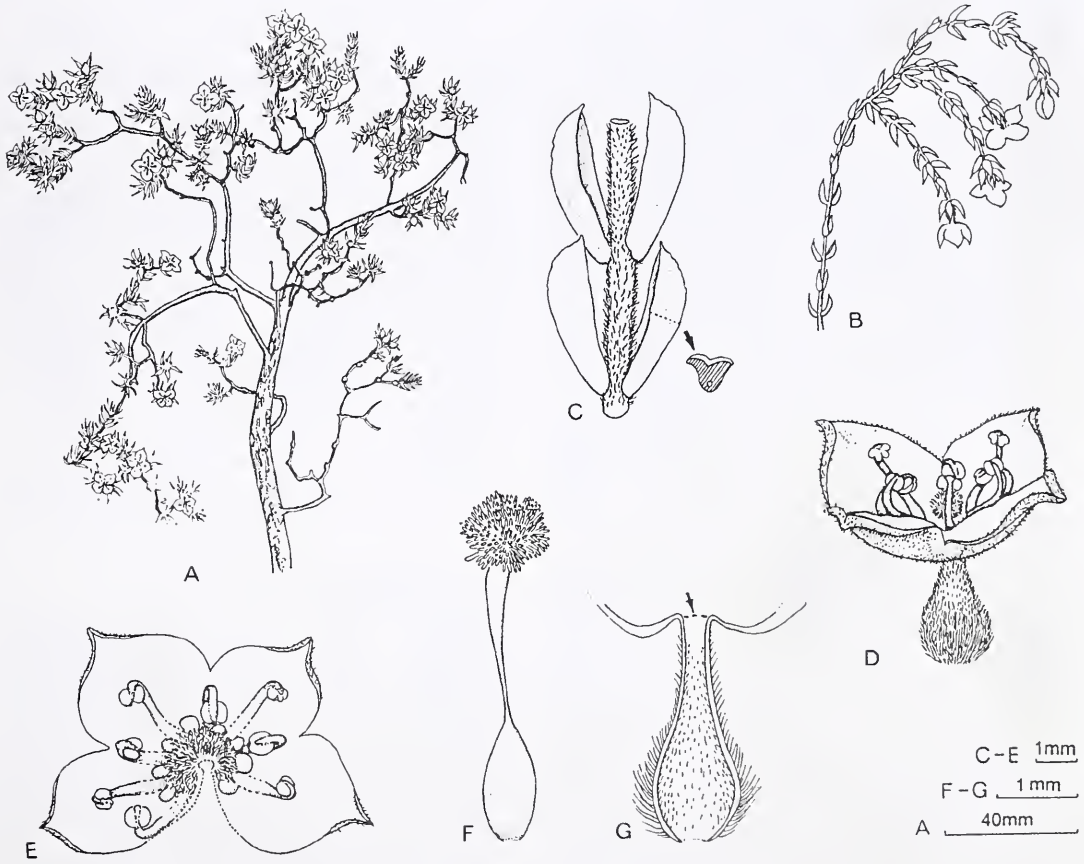

FIGURE 24.—*Lachnaea pudens*, *Beyers 161* (NBG). A, portion of plant; B, flowering branch, × 1; C, branch with leaves and c/s leaf. D, E, flower; E, upper portion above circumscission zone. F, gynoecium; G, l/s portion of hypanthium, showing basal invagination of upper portion just above circumscission zone (arrowed). Scale bars: A, 40 mm; C–G, 1 mm.

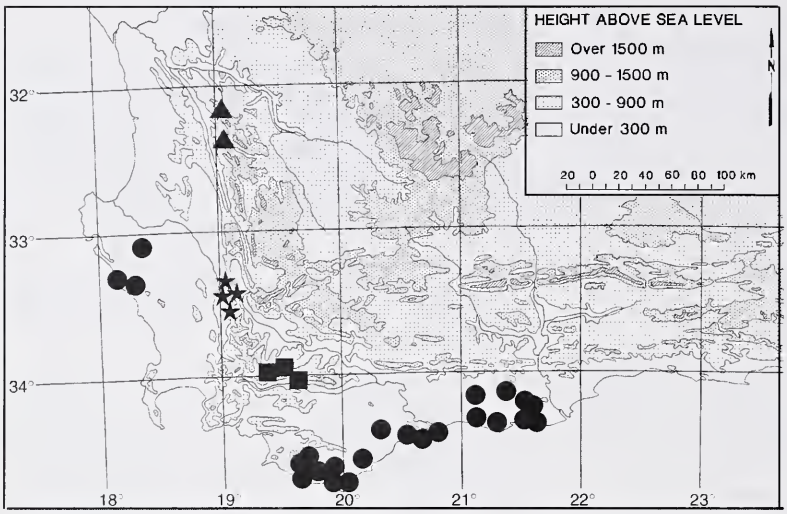

FIGURE 25.—Known distribution of *Lachnaea pudens*, ■; *L. axillaris*, ●; *L. leipoldtii*, ▲; *L. pusilla*, ★.

Radojitskya capensis Turcz.: 176 (1852); Turcz.: 743 (1853). Type: Cape of Good Hope, *Zeyher 2163* (S, holo.!; K!, NBG!, iso.).

Erect, much-branched, compact shrub up to 0.75 m tall, multistemmed at base; resprouter. *Branches* erect to flexuous and interlacing, filiform, ± terete, internodes ± as long as leaves, sericeous or sericeous-tomentose, leafy, becoming puberulent and naked without prominent leaf scars. *Leaves* decussate with distal 2 pairs of leaves sometimes subverticillate, ascending, distant, sessile, epistomatic, narrowly ovate to lanceolate, 2–4 × 0.8–1.2 mm, fleshy, glabrous; adaxially flat, smooth, dull, ± white-punctate; abaxially convex, subkeeled towards apex, glossy; apex mucronate; base obtuse. *Inflorescence* terminal, 1-flowered, but may appear axillary when much reduced, lateral branches comprise only one pair of leaves and a single flower, sericeous to sericeous-tomentose at floral articulation. *Flowers* sessile, subactinomorphic, cream, pink or dark pink. *Hypanthium* 1.4–2.2 mm long, circumscissile $^1/_2$–$^2/_3$ from base; upper portion cup-shaped with a basal invagination; basal portion ovoid to broadly ovoid, glabrous outside, glabrous inside but barbate above circumscission zone in vicinity of floral scales. *Sepals* erect-spreading, subequal, 2 outer ones elliptic, ovate to broadly ovate, 1.6–2.6 × 0.8–1.5 mm, acute, adaxially glabrous or near apex puberulent or ciliolate, abaxially glabrous, 2 inner ones elliptic, obovate to broadly obovate, acute to obtuse, 1.4–2.3 × 1.0–1.8 mm, adaxially glabrous becoming puberulent near apex, abaxially glabrous. *Stamens* exserted, outer, antesepalous whorl arising at base of sepals, inner, antepctalous whorl arising at mouth of hypanthium; filaments 0.4–0.8 mm long, inner whorl shorter or as long as outer whorl; anthers widely ellipsoid to spheroid, 0.4–0.5 mm long, dorsally with broad connective tissue. *Floral scales* arising just above circumscission zone immediately below antepctalous stamens, partially concealed by stiff hairs in throat of hypanthium, subrotund, 0.2–0.4 mm long, glabrous. *Ovary* narrowly ellipsoid to ellipsoid, 1.0–1.3 mm long, glabrous. *Style* teretc-obconical, 0.8–1.6 mm long, glabrous. *Stigma* capitate and papillate (Figure 26).

Distribution and ecology

Confined to the Western Cape and with a disjunct distribution. Occurs on sandy flats in the Hopefield and Darling Districts in the southwestern area and re-appears along the southern coast from Elim to the Gourits River mouth (Figure 25). The distribution of *L. axillaris* requires some explanation. The southern coastal flats are separated from the western coastal flats by a formidable ecological barrier, namely the Hottentots Holland Mountains. At the present time there are no low-lying coastal sandy areas which could link the two areas of distribution. Rourke (1972) hypothesized that due to coastline regression during the Middle Pleistocene, a lowland link, now inundated, provided a migration route between the Bredasdorp coastal flats and the Cape Flats. *Flowering time*: throughout the year.

Conservation status: Vulnerable (VU A1ce). The habitat of this species has been restricted through the effects of human activities and invasion by alien invader plants.

Diagnostic characters and relationships

Lachnaea axillaris is closely related to *L. pudens*, *L. leipoldtii* and *L. pusilla*. The upper portion of the hypanthium in these species is basally invaginated. *L. axillaris* is easily distinguished from *L. pudens* by the hypanthium being glabrous on the outside. In *L. axillaris* the upper portion of the hypanthium is cup-shaped and the stigma is capitate and papillatc, whereas in *L. leipoldtii* and *L. pusilla* it is narrowly obconical and the stigma is conical and papillate and narrowly conical and papillate respectively.

Vouchers: *Bayliss 6608* (GRA, K, NBG, NY, S, Z); *Bevers 127* (NBG); *Esterhuysen 23265* (BOL, PRE); *Hugo 1613* (NBG, PRE); *McDonald 1395* (K, MO, NBG, PRE); *Spreeth 160* (K, MO, NBG, PRE). Total number of specimens examined: 139.

7. **Lachnaea leipoldtii** *Beyers*, sp. nov., *L. axillaris* parte superiore hypanthii basaliter invaginata affinis, sed differt parte superiore hypanthii obconica (non cyathiformi) stigmate conico (non capitato).

TYPE.—Western Cape, 3219 (Wuppertal): northern Cederberg, between Heuningvlei and Boontjieskloof in moist, sandy flats between Heuningvlei and Koupoort, ± 950 m, (–AA), 28-12-1983, *Taylor 10871* (NBG, holo.!; PRE!, iso.).

Erect to decumbent, much-branched shrub up to 0.4 m tall, single-stemmed at base, branching close to ground; reseeder. *Branches* ascending to patent, flexuous, slender, terete, internodes $^3/_4$–$1^1/_2$ as long as leaves, tomentose, leafy, becoming sparsely hairy and naked without prominent leaf scars. *Leaves* decussate with distal 2 pairs of leaves subverticillate, adpressed, scattered, sessile, epistomatic, narrowly elliptic to ovate, 2.2–3.5 × 0.8–1.2 mm, coriaceous, glabrous: adaxially concave, enervate, dull, ± white-punctate; abaxially convex, keeled, glossy, enervate;

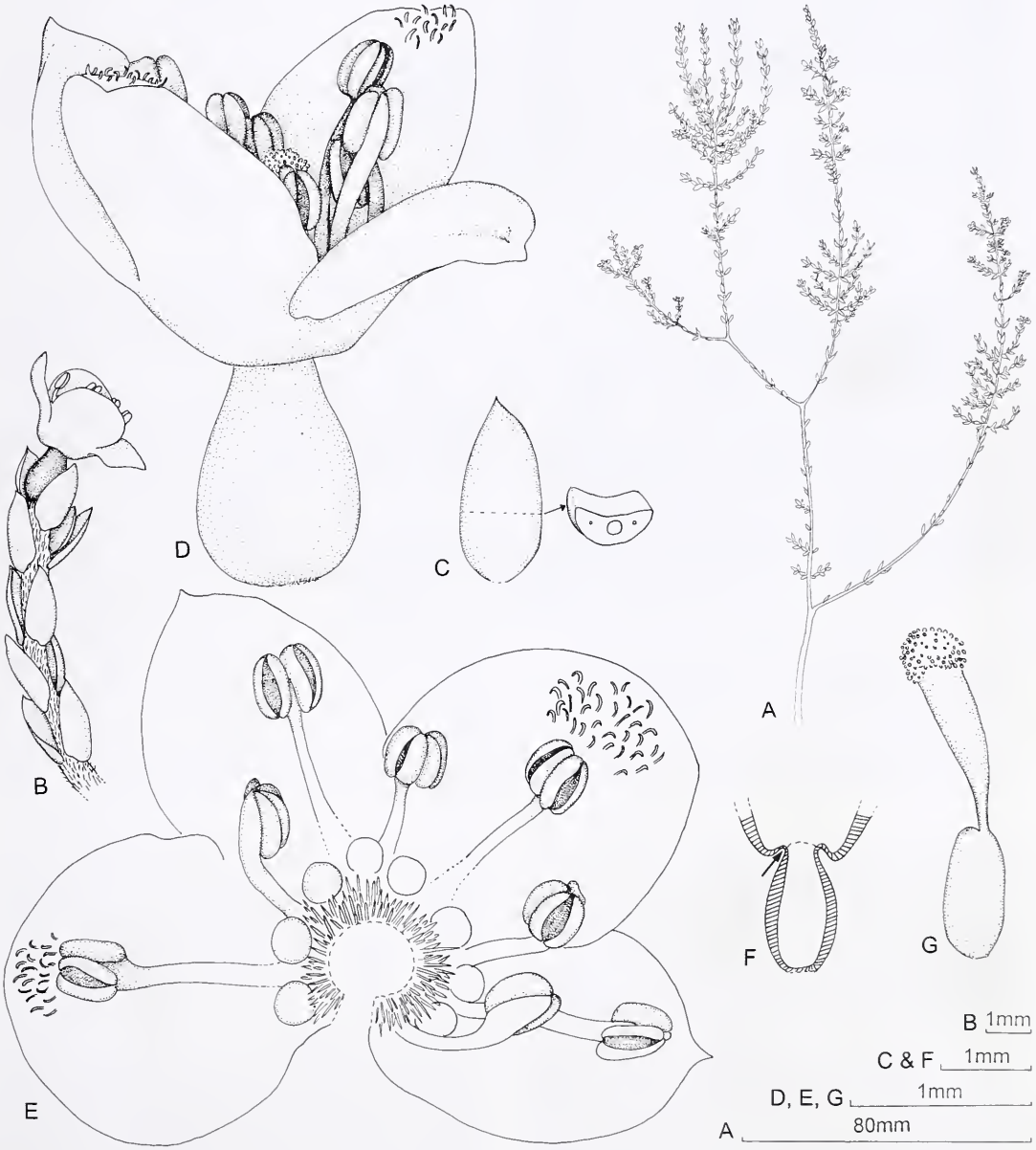

FIGURE 26.—*Lachnaea axillaris*, *Beyers 180* (NBG). A, portion of plant; B, flowering branch; C, leaf, abaxial view and c/s. D, E, flower: E, l/s upper portion above circumscission zone. F, l/s hypanthium and circumscission zone arrowed; G, gynoecium. Scale bars: A, 80 mm; B–G, 1 mm.

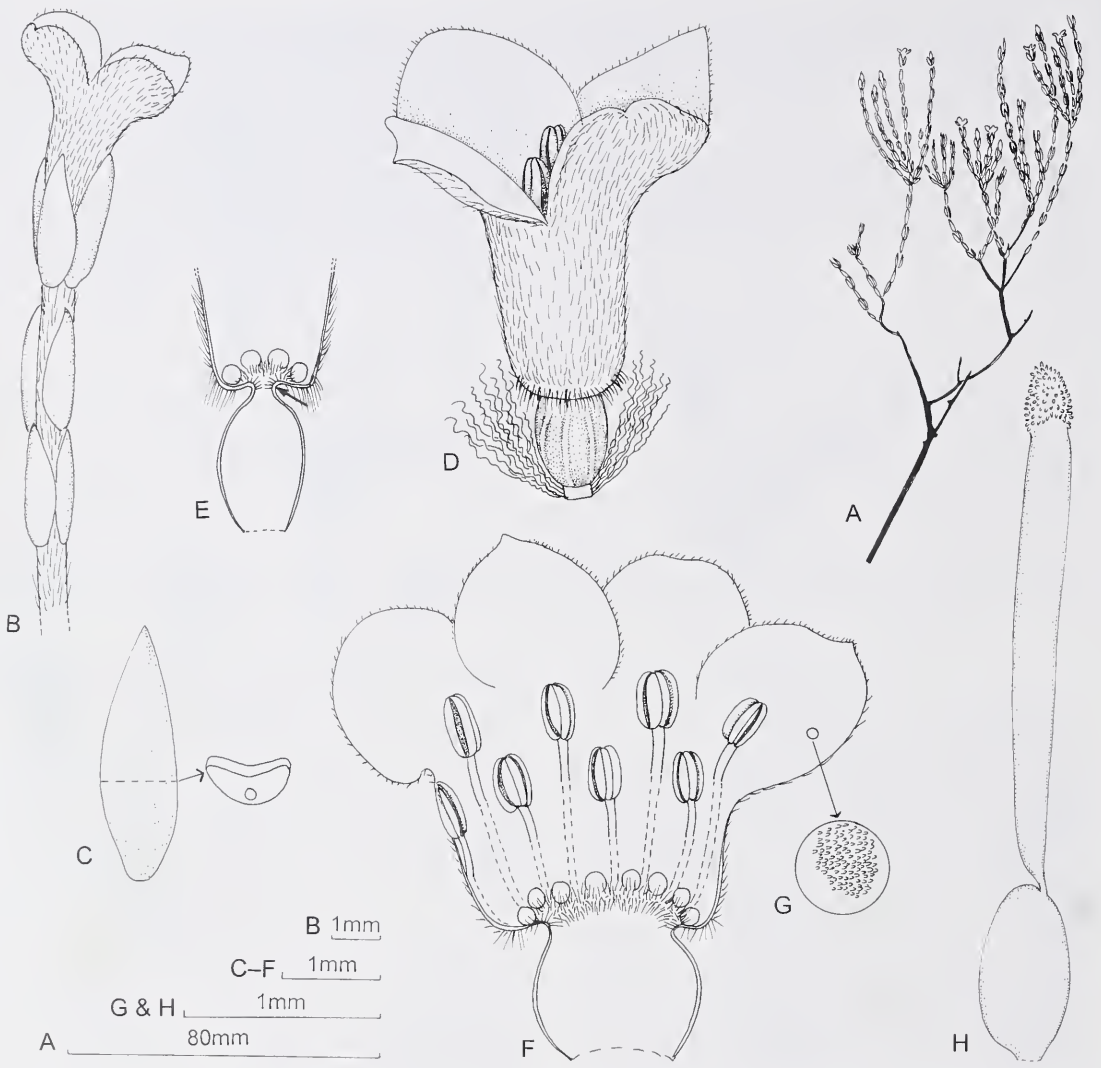

FIGURE 27.—*Lachnaea leipoldtii*, *Taylor 10871* (NBG). A, portion of plant; B, flowering branch; C, leaf, abaxial view and c/s; E, l/s hypanthium and circumscission zone arrowed. D, F, flower; F, l/s with gynoecium removed. G, inner surface of sepal papillate; I, gynoecium. Scale bars: A, 80 mm; B–H, 1 mm.

apex acute; base rounded. *Inflorescence* terminal, 1-flowered, sericeous-villous at floral articulation. *Flowers* sessile, subactinomorphic, white. *Hypanthium* 2.6–3.6 mm long, circumscissile $^1/_3$ from base; upper portion narrowly obconical with basal invagination, sericeous outside, but at basal invagination hairs retrorse, glabrous inside but barbate at circumscission zone; basal portion ellipsoid or obovoid, glabrous outside and inside. *Sepals* ascending, subequal, very widely ovate to oblate, 1.5–2.0 × 1.5–1.9 mm, apex rounded to obtuse, sericeous abaxially, glabrous adaxially. *Stamens*: outer, antesepalous whorl exserted or half exserted, arising $^1/_6$–$^1/_4$ down upper portion of hypanthium, inner, antepetalous whorl enclosed, arising $^2/_3$ down upper portion of hypanthium; filaments usually shorter than anthers, 0.3–0.7 mm long, inner whorl usually as long as outer whorl; anthers ellipsoid to widely ellipsoid, 0.5–0.8 mm long, dorsally with broad connective tissue. *Floral scales* included, arising just above circumscission zone partially concealed by stiff hairs at base, subglobose, ± 0.2 mm long, glabrous. *Ovary* ellipsoid, 0.5–1.0 mm long, glabrous. *Style* terete-obconical, 0.9–2.4 mm long, glabrous. *Stigma* conical and papillate (Figure 27).

Distribution and ecology

Lachnaea leipoldtii is endemic to the northern Cederberg. It favours moist, sandy areas at an altitude of ± 1 000 m (Figure 25). *Flowering time*: December and February.

Conservation status: Vulnerable (VU D2). This species has a restricted distribution and being a reseeder would be vulnerable to frequent mountain fires.

Diagnostic characters and relationships

Lachnaea leipoldtii is allied to *L. axillaris* with the upper portion of the hypanthium basally invaginated, but differs in that the upper portion of the hypanthium is narrowly obconical and not cup-shaped and the stigma is conical and papillate and not capitate and papillate. *L. leipoldtii* is sister to *L. pusilla* but differs in that the basal portion of the hypanthium is glabrous outside and the stigma is conical and papillate.

Eponymy

This species was first collected in 1889 by Dr C. L. Leipoldt, the renowned Afrikaans poet and keen amateur botanist. Since the first collection, three other collections have been made close to his grave, thus prompting the choice of the specific epithet.

Vouchers: *Esterhuysen 34831* (BOL), *7523* (BOL); *Leipoldt 1047* (BOL). Total number of specimens examined: 5.

8. **Lachnaea pusilla** *Beyers*, sp. nov., *L. leipoldtii* proxime affinis, sed differt parte basali hypanthii extra pilis obtusis in parte superiore (non omnino glabra), stigmate peranguste conico (non conico).

TYPE.—Western Cape, 3319 (Worcester): Wellington Dist., Elandsberg Private Nature Reserve, in restioid flats between Elandskloof Mountains and fields in Tortoise Reserve, 70 m, (–AC), 4-10-1994, *Beyers 243* (NBG, holo.!; BOL!, K!, MO!, NY!, PRE!, S!; Z!, iso.).

Straggling, erect, much-branched shrub up to 0.4 m tall, single-stemmed at base; reseeder. *Branches* ascending to patent, flexuous, filiform, terete, internodes $^3/_4$ to as long as leaves, sericeous, leafy, becoming glabrous and naked without prominent leaf scars. *Leaves* decussate with distal 2 pairs of leaves subverticillate, adpressed, sessile, epistomatic, narrowly elliptic, 2.8–3.2 × 0.6–0.7 mm, coriaceous, glabrous; adaxially concave, enervate, dull, ± white-punctate; abaxially convex, subkeeled, glossy; apex subacute; base rounded. *Inflorescence* terminal, 1-flowered, villous at floral articulation. *Flowers* sessile, subactinomorphic, white, some tinged pale pink. *Hypanthium* 2.3–3.2 mm long, circumscissile $^1/_4$–$^1/_3$ from base; upper portion narrowly obconical with basal invagination, sericeous outside, but at basal invagination hairs retrorse, inside sericeous at mouth, glabrescent towards base and barbate at base of floral scales; basal portion ellipsoid or obovoid, outside puberulent in upper and lower $^1/_3$, middle portion covered with ascending, obtuse hairs, inside adpressed hairy at plane of circumscission, glabrous below. *Sepals* erect-patent, subequal, elliptic to widely elliptic, 1.4–2.5 × 1.2–1.7 mm, rounded to obtuse, sericeous on both sides. *Stamens*: outer, antesepalous whorl exserted, arising at mouth of hypanthium; inner, antepetalous whorl enclosed, arising $^2/_5$ way down upper portion of hypanthium; filaments as long or shorter than anthers, 0.2–0.5 mm long, inner whorl shorter or as long as outer whorl; anthers ellipsoid to ovoid, 0.5–0.7 mm long, dorsally with broad connective tissue. *Floral scales* included, arising just above circumscission zone partially concealed by stiff hairs at base, subglobose, 0.2–0.3 mm long, glabrous, yellow in fresh state. *Ovary* ellipsoid, 0.8–0.9 mm long, glabrous. *Style* narrowly cylindrical-obconical, 0.7–1.0 mm long, glabrous. *Stigma* very narrowly conical, papillate, 1.6–2.0 mm long (Figure 28).

Distribution and ecology

Recorded from Nuwekloof southwest of Tulbagh southwards along Elandskloof Mountains to the western foot of Bailey's Peak north of Wellington, occurring in stony sand between 70 and 1 000 m above sea level (Figure 25). *Flowering time*: from October to March.

Conservation status: Vulnerable (VU D2). This species has a restricted distribution and although also occurring in a private nature reserve, would be vulnerable to frequent fires as it is a reseeder.

Diagnostic characters and relationships

Lachnaea pusilla is closely allied to *L. leipoldtii* but differs in that the basal portion of the hypanthium outside is covered with obtuse hairs in the upper half and the stigma is very narrowly conical and papillate.

Etymology

The specific epithet, means very small, and refers to the tiny flowers.

Vouchers: *De Villiers 45* (NBG); *Esterhuysen 22341* (BOL, PRE); *Schlechter 1195* (PRE), *7503* (BOL; GRA; K; S; Z). Total number of specimens examined: 17.

9. **Lachnaea laxa** (*C.H.Wright*) *Beyers* in Bothalia 27: 45 (1997). *Cryptadenia laxa* C.H.Wright: 17 (1915). Syntypes: Caledon Div., Swartberg, near Caledon, 3200 ft, *Bolus 7875* (BOL!); near Houw Hoek, 2000 ft, *Bolus 9208* (BOL!); Bredasdorp Div., near Elim, *Bolus 7876* (BOL!, PRE!); without locality, *Harvey s.n.* (K, lecto.!, here designated; K!, isolecto.).

Note: Wright cites the locality of *Bolus 9208* as 'near Houw Hoek, 2000 ft'. Only the sheet in BOL has the collecting no. 9208, but with a question mark behind the locality and there is no date. Sheets of *Bolus HNAA1353* (BOL, K, NBG, SAM, Z) correspond to the locality and altitude given by Wright [sheet in BOL determined by Wright] for *Bolus 9208*. Unfortunately one cannot assume that they were used in the preparation of the protologue. *Harvey s.n. sub herb. Hooker* (K) is selected as the lectotype, as it was determined by Wright. The isolectotype is mounted on the same sheet as *Bolus HNAA1353* (K).

Erect to decumbent, sparsely to moderately branched shrub up to 0.3 m tall, single-stemmed at base, branching close to ground; reseeder. *Branches* slender, lax to straggling, ridged below leaf bases, internodes $^3/_4$–$1^1/_3$ as long as leaves, at first sericeous, leafy, later glabrescent and naked with inconspicuous leaf scars. *Leaves* decussate with distal 2 pairs of leaves subverticillate, adpressed to ascending, scattered, sessile, narrowly

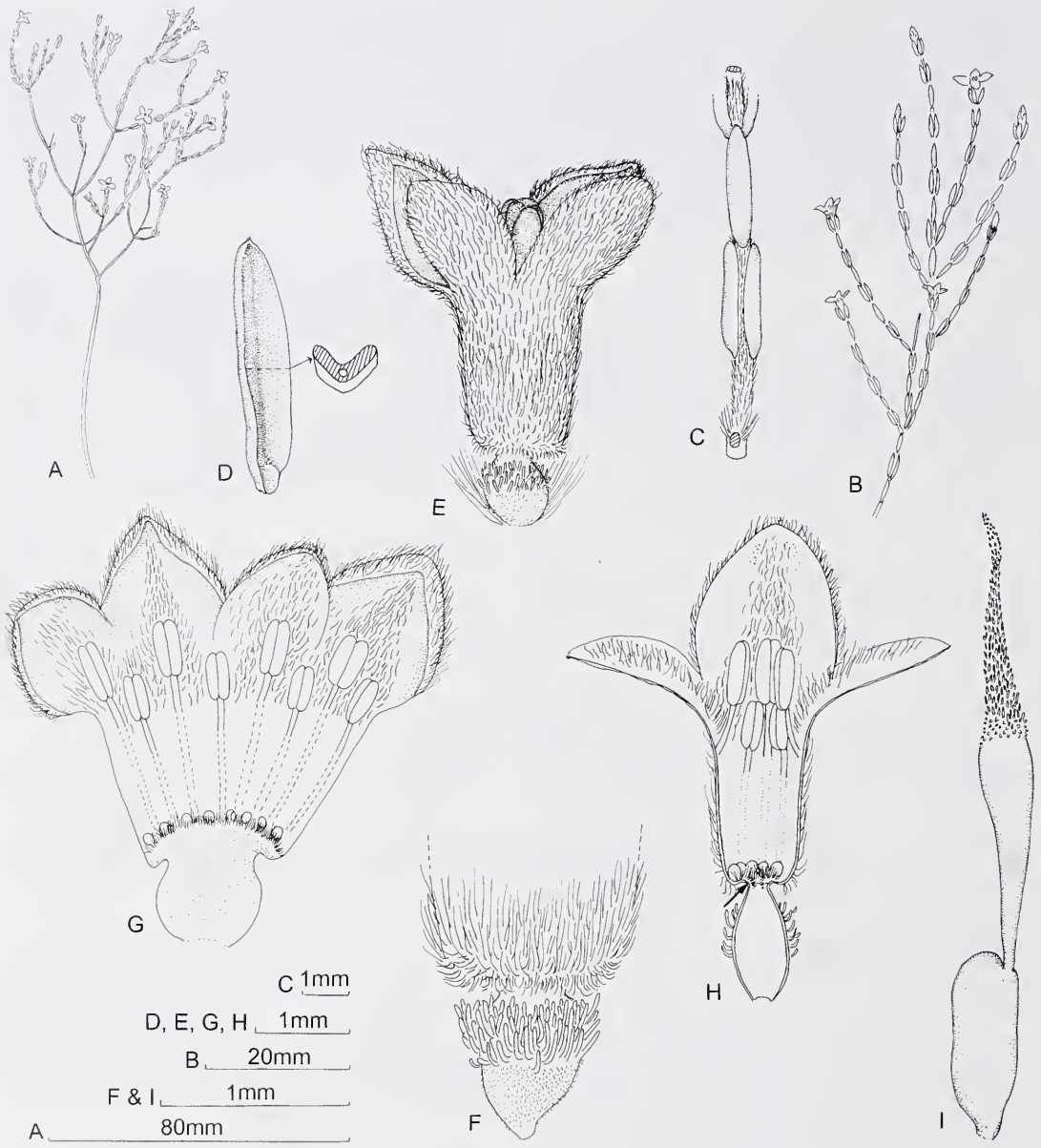

FIGURE 28.—*Lachnaea pusilla*, *Beyers 243* (NBG). A, portion of plant; B, portion of plant; C, branch with leaves; D leaf, lateral view and c/s; F, hypanthium. E, G, H, flower: G, l/s with gynoecium removed; H, l/s and circumscission zone arrowed. I, gynoecium. Scale bars: A, 80 mm; B, 20 mm; C–I, 1 mm.

elliptic to lanceolate, 3.8–7.6 × 0.6–1.3 mm, coriaceous, glabrous; adaxially concave, smooth, dull, ± white-punctate; abaxially convex, smooth or keeled, glossy; apex acute; base obtuse. *Inflorescence* terminal, 1-flowered, sericeous at floral articulation. *Flowers* sessile, subactinomorphic, cream to pink. *Hypanthium* 3.8–8.0 mm long, circumscissile ± $^1/_3$ from base; upper portion funnel-shaped; basal portion narrowly ovoid, sericeous outside; upper portion adpressed hairy inside; basal portion glabrous inside. *Sepals* erect-patent, subequal, narrowly elliptic to elliptic, 2.8–8.5 × 1.3–4.2 mm, acute to subacute, abaxially sericeous, adaxially sparsely sericeous or sericeous only in upper $^1/_4$, lower $^3/_4$ glabrous. *Stamens* exserted; outer, antesepalous whorl arising at base to lower $^1/_5$ of sepals; inner, antepetalous whorl arising at rim of hypanthium; filaments 0.4–2.0 mm long, inner shorter than outer whorl; anthers ellipsoid, 0.6–1.2 mm long, abaxially without broad connective tissue. *Floral scales* exserted, arising at mouth of hypanthium just below antepetalous stamens, narrowly ellipsoid, 0.5–1.3 mm long, glabrous, translucent-white in fresh state. *Ovary* narrowly ellipsoid to ellipsoid or obovoid,

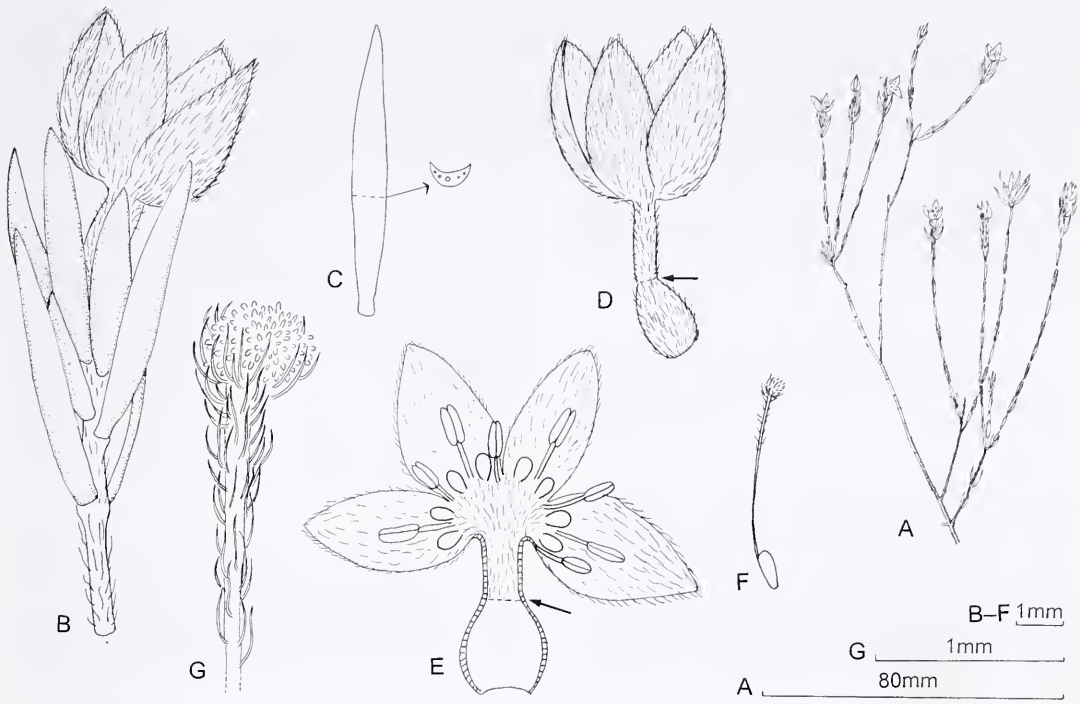

FIGURE 29.—*Lachnaea laxa*, *I. Oliver 4* (NBG). A, portion of plant; B, flowering branch; C, leaf, abaxial view and c/s. D, E, flower: D, circumscission zone arrowed; E, l/s with gynoecium removed. F, gynoecium; G, stigma and upper portion of style. Scale bars: A, 80 mm; B–G, 1 mm.

0.8–1.2 mm long, glabrous. *Style* linear, 2.8–6.0 mm long, covered with soft, ascending hairs in upper half. *Stigma* brush-like (Figure 29).

Distribution and ecology

Recorded from the Jonkershoek and Hottentots Holland Mountains eastwards to Genadendal and southeast to the Houhoek Mountains and Swartberg, above Caledon. It has also been recorded from Elim but no precise locality is given. It occurs on mid to upper slopes, at altitudes between 400 and 2 150 m, favouring damp, sandy areas (Figure 30). *Flowering time*: October to December.

Conservation status: Vulnerable (VU D2). Judging by the few known collections, most of which are old, it occurs in a restricted area on high mountains. From the available collections it appears to be a reseeder and would therefore be vulnerable to frequent fires.

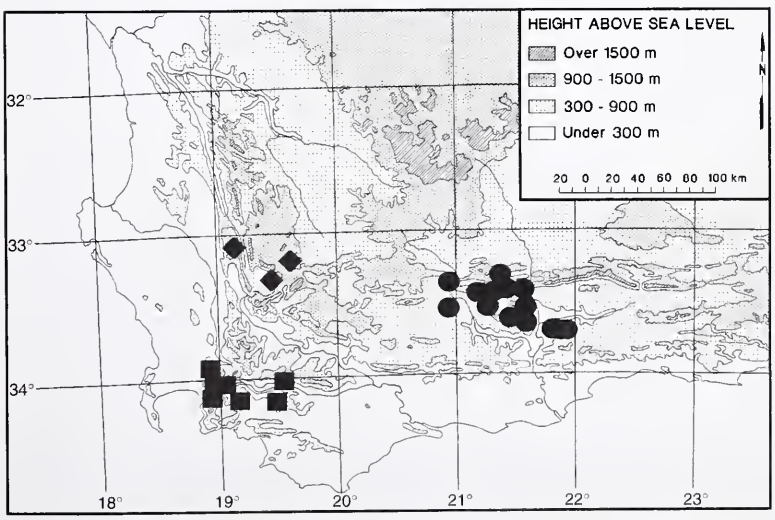

FIGURE 30.—Known distribution of *Lachnaea laxa*, ■, *L. rusci-folia*, ●; *L. alpina*, ◆.

Diagnostic characters

Lachnaea laxa is easily distinguished from the other solitary-flowered species with a decussate leaf arrangement and cream to pink flowers, by the upper portion of the hypanthium being funnel-shaped and the floral scales arising at the mouth of the hypanthium.

Vouchers: *Bolus HNAA1353* (BOL, K, NBG, SAM, Z); *Boucher 2637* (NBG); *Esterhuysen 17598* (BOL, NBG); *A. Johns 5* (NBG); *I. Oliver 4* (NBG, PRE); *Schlechter 5444* (GRA, Z). Total number of specimens examined: 22.

10. **Lachnaea ruscifolia** *Compton* in Journal of South African Botany 19: 132 (1953). Type: Western Cape, 3321 (Ladismith): Klein Swartberg Range, Elandsberg, 2000 ft, (–AD), July/August 1953, *Wurts 1036* (NBG, holo.!; K!, PRE!, iso.).

Erect, moderately branched shrub up to 0.8 m tall, multistemmed at base; resprouter. *Branches* erect, slender to moderately thick, ridged below leaf bases, covered with long, straight, adpressed hairs admixed with crooked ones, densely leafy, later glabrescent and naked with prominent leaf scars. *Leaves* alternate, ascending to patent, imbricate, sessile to subsessile, epistomatic, ovate to orbicular, 5.0–10.5 × 2.6–5.5 mm, coriaceous, green, glabrous; adaxially obtusely concave, smooth, dull, ± white-punctate; abaxially convex, glossy, with 6–9 ridges converging to base and apex; apex acute to subacute; base cuneate, margin indurated, at first pilose, later deciduous, becoming naked; petiole up to 0.6 mm long. *Inflorescence* terminal, 1-flowered, but appearing to be axillary as apical meristem of main branches seems to abort and flowers borne only on much reduced, lateral flowering shoots, comprising usually one pair of small, scarious, bracteose leaves and a solitary flower, which develop at random in axils of foliage leaves on main flowering branches thus appearing spicate-like. *Flowers* sessile, subactinomorphic, creamy white. *Hypanthium* 2.7–4.7 mm long, circumscissile $^1/_3$ from base; upper portion narrowly funnel-shaped, tomentose outside, adpressed villous inside; basal portion ellipsoid, tomentose outside, glabrous inside. *Sepals* ascending, subequal, elliptic to narrowly ovate, 2.8–4.5 × 1.5–2.2 mm, subacute to obtuse, both surfaces tomentose. *Stamens* exserted; outer, antesepalous whorl arising at base of sepals, 0.9–1.3 mm long; inner, antepetalous whorl arising at rim of hypanthium, 0.9–1.1 mm long; anthers spheroid, 0.3–0.5 mm long, abaxially without broad connective tissue. *Floral scales* exserted, arising at mouth of hypanthium, immediately below antepeta-

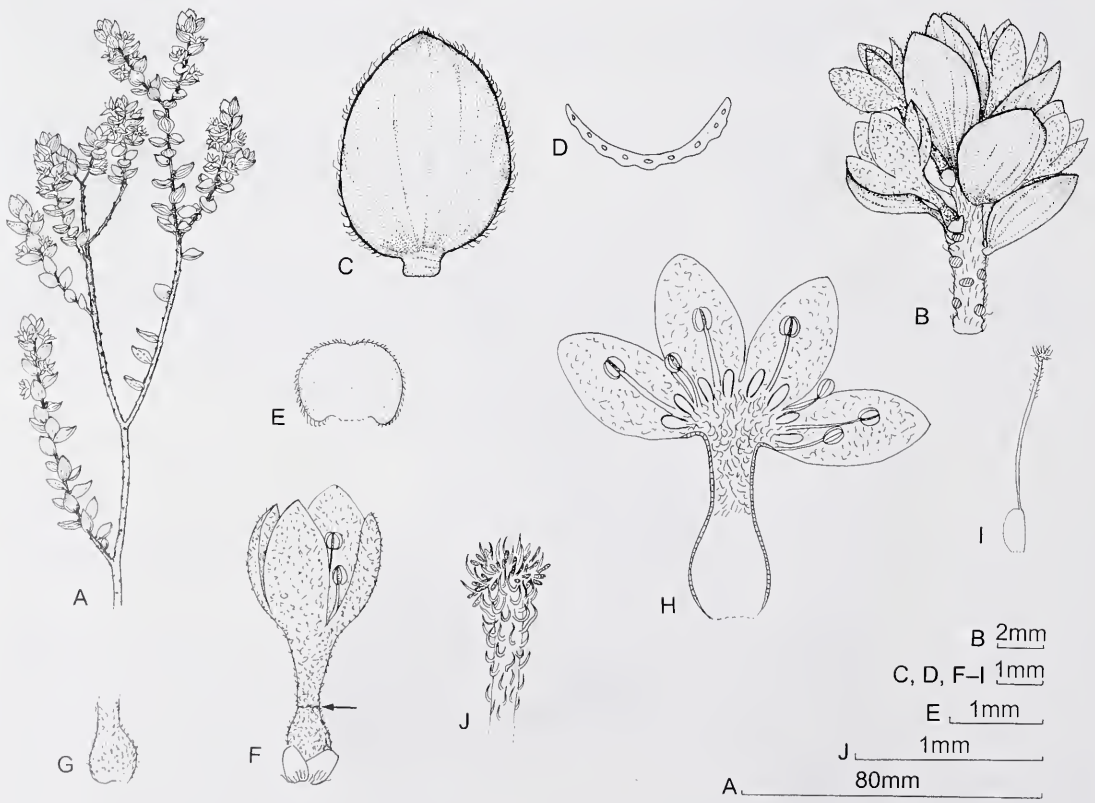

FIGURE 31.—*Lachnaea ruscifolia, Vlok 2084* (NBG). A, portion of plant; B, flowering branch. C–E, leaf: C, abaxial view; D, c/s; E, scarious, bracteose. F, H, flower: F, with bracteose leaves at base and circumscission zone arrowed; H, l/s with gynoecium removed. G, basal portion of hypanthium; I, gynoecium; J, stigma and upper portion of style. Scale bars: A, 80 mm; B, 2 mm; C–J, 1 mm.

lous stamens, ovate to obovate in outline, laterally flattened, 0.6–1.0 mm long, glabrous, yellow in fresh state. *Ovary* ovoid, 0.8–1.1 mm long, usually glabrous but occasionally with tuft of hair at base of style. *Style* terete-obconical, 2.7–4.5 mm long, with incurled hairs in upper half, rest glabrous. *Stigma* capitate, elongate-papillate (Figure 31).

Distribution and ecology

Confined to the mountains of the Little Karoo, from the Klein Swartberg and Rooiberg in the west to the Groot Swartberg and Gamka Mountain in the east, at altitudes between 650 and 1 150 m, growing in rocky, sandy loam soils (Figure 30). *Flowering time*: December to September.

Conservation status: Lower Risk Least Concern (LRlc).

Diagnostic characters

Lachnaea ruscifolia is easily distinguished from the other 1-flowered species by the alternate, ovate to orbicular leaves with six to nine prominent ridges below the leaves.

Vouchers: *Cattell & Cattell 230* (NBG); *Esterhuysen 25893* (BOL); *Oliver 10360* (NBG); *Vlok 1898* (NBG, PRE), *2084* (NBG, PRE); *Wurts 1342* (NBG). Total number of specimens examined: 43.

11. **Lachnaea alpina** *(Eckl. & Zeyh.) Meisn.* in DC., Prodromus systematis naturalis regni vegetabilis 14: 578 (1857); C.H.Wright: 583 (1925). Type: in mountain Winterhoeksberg, near Tulbagh, alt. 6000 ft, *Ecklon s.n.* (NY, holo.!; S!, SAM!, iso.).

Gonophylla alpina Eckl. & Zeyh. ex Meisn.: 578 (1857) nom. nud. in synonymy.

Erect, much-branched shrub up to 1 m tall, single-stemmed at base with capacity to sprout from base of old branches; reseeder. *Branches* ascending, slender, later becoming woody, ridged below leaf bases, glabrous or at first hirsute below inflorescence becoming glabrous, densely leafy, becoming naked with prominent leaf scars. *Leaves* alternate, ascending, imbricate, subsessile, epistomatic, glabrous, narrowly elliptic to obovate, 5–10 × 1.5–3.0 mm, coriaceous, green, faintly midveined; adaxially flat or obtusely concave, dull, white-punctate; abaxially flat or obtusely convex, glossy, smooth; apex rounded to acute, straight or slightly incurved; base attenuate. *Inflorescence* a terminal, ebracteate capitulum, 15–25 mm diam., ± 12–40-flowered, pedunculate; peduncle 3–20 mm long, sericeous-hirsute. *Receptacle* subconical, 2.0–3.2 × 2.2–3.5 mm, sericeous. *Flowers* sessile, subactinomorphic to zygomorphic, pale blue, mauve or cream, strongly honey-scented. *Hypanthium* 4.3–6.8 mm long, circumscissile $^1/_3$–$^1/_2$ from base; upper portion funnel-shaped; basal portion ellipsoid, sericeous-villosulous outside, adpressed hairy inside above plane of circumscission, glabrous below. *Sepals* patent, equal to unequal, abaxially sericeous-villosulous, adaxially sericeous, elliptic, ovate or obovate, apex acute to rounded, anterior and lateral sepals ± equal, 2.9–5.4 × 1.4–3.0, posterior one smallest, 2.1–3.8 × 1.3–3.0 mm. *Stamens* exserted; outer, antesepalous whorl arising near base of sepals; inner, antepetalous whorl arising at rim of hypanthium; filaments 0.7–2.0 mm long, inner whorl as long as or slightly shorter than outer whorl; anthers depressed spheroid, 0.4–0.5 mm long, abaxially without broad connective tissue. *Floral scales* exserted, arising at mouth of hypanthium immediately below antepetalous stamens, obovoid, 0.4–0.6 mm long, hirsute, yellow in fresh state. *Ovary* obovoid, 0.9–1.5 mm long, apex sericeous, glabrous below. *Style* filiform, covered with silky, ascending hairs. *Stigma* brush-like (Figure 32).

Distribution and ecology

Lachnaea alpina is known only from the mountains in the Tulbagh and Ceres Districts, occurring at altitudes between 1 600 and 2 100 m (Figure 30). *Flowering time*: November to January.

Conservation status: Vulnerable (VU D2). This species has a restricted distribution, and being a reseeder is vulnerable to frequent mountain fires.

Diagnostic characters and relationships

Lachnaea alpina belongs to the group of species with capitate inflorescences. It is easily distinguished from *L. macrantha*, the only other species in this group which also has epistomatic leaves, by its honey-scented, subactinomorphic to slightly zygomorphic flowers, with the posterior sepal either equal to or slightly shorter than the other sepals.

Vouchers: *Beyers 258* (K, MO, NBG, PRE); *Bond 1454* (BOL); *Esterhuysen 19799* (BOL, PRE), *29830* (BOL); *Forsyth 508* (NBG); *Oliver 9299* (BOL, K, NBG, PRE). Total number of specimens examined: 26.

12. **Lachnaea macrantha** *Meisn.* in DC., Prodromus systematis naturalis regni vegetabilis 14: 575 (1857); C.H.Wright: 19 (1915). Type: Cape, without locality, *Ecklon & Zeyher s.n.* ['28. *Lachnaea buxifolia.Eckl. & Zeyh. L. macrantha nob.*'–scrips. Meisn.] (S, holo.!).

Lachnaea buxifolia Eckl. & Zeyh. ex Meisn.: 575 (1857) nom. nud. in synonymy.

Erect to semi-erect, sparsely to much-branched shrub up to 2 m tall, single-stemmed at base; reseeder. *Branches* ascending, woody, ridged below leaf bases, glabrous, leafy, becoming naked with prominent leaf scars. *Leaves* alternate, ascending, those lower down on stem sometimes patent, imbricate, subsessile, epistomatic, obovate, 7–23 × 2.9–11.0 mm, coriaceous, glabrous, faintly nerved; adaxially ± flat or obtusely concave, glaucous, white-punctulate; abaxially ± flat or obtusely convex, glossy, smooth; apex rounded or mucronulate; base cuneate. *Inflorescence* a terminal, more than 50-flowered,

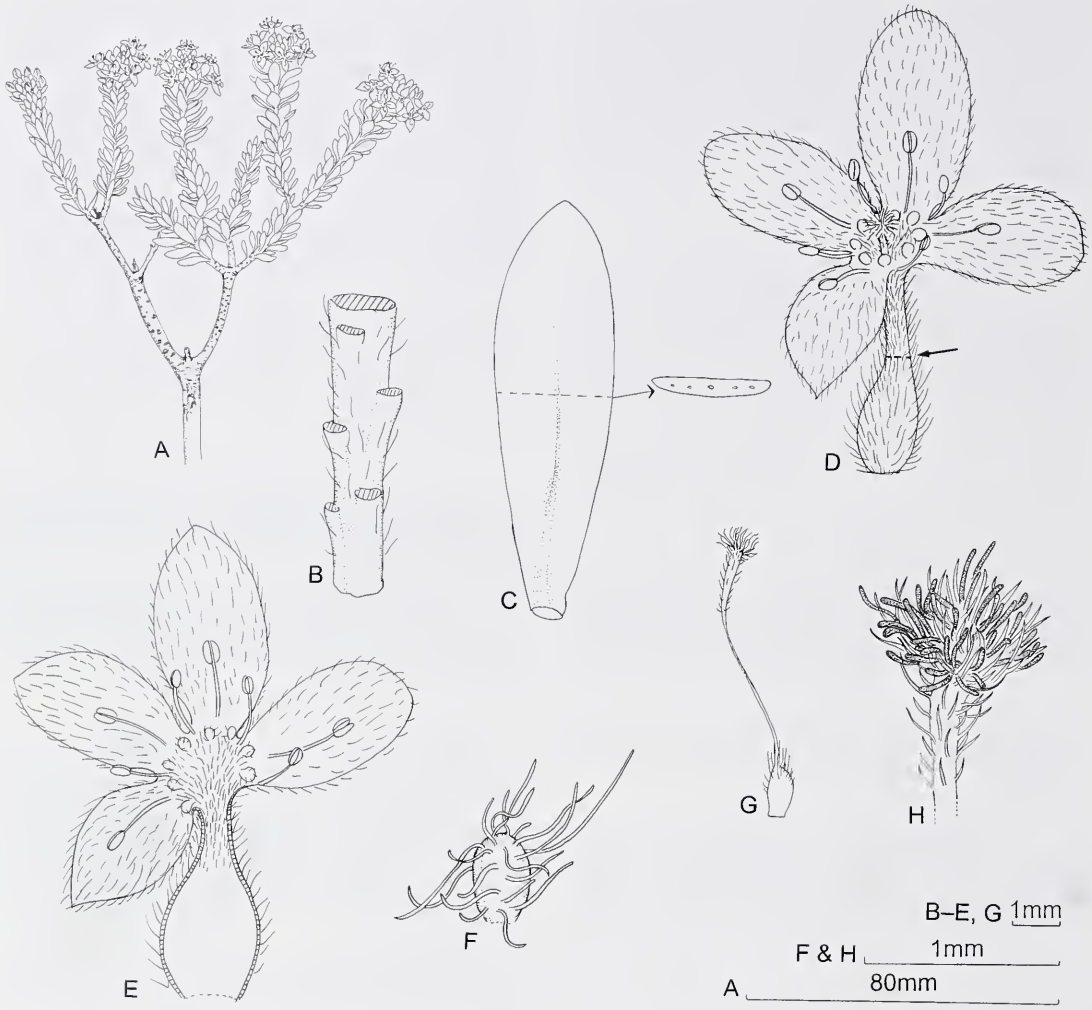

FIGURE 32.—*Lachnaea alpina*, *Beyers 258* (NBG). A, portion of plant; B, branch with leaves removed; C, leaf, abaxial view and c/s. D, E, flower: D, circumscission zone arrowed; E, l/s with gynoecium removed. F, scale; G, gynoecium; H, stigma and upper portion of style. Scale bars: A, 80 mm; B–H, 1 mm.

ebracteate capitulum, 35–60 mm diam., basally enclosed by foliage leaves, pedunculate; peduncle 2–3 mm long, puberulent towards apex, glabrous below. *Receptacle* oblong conical to ellipsoid, 4.0–5.5 × 1.8–2.2 mm, puberulent. *Flowers* sessile, zygomorphic, cream, occasionally with pink or purplish tint, fragrantly scented. *Hypanthium* 6.6–10.6 mm long, circumscissile ± $^1/_2$ way; upper portion narrowly funnel-shaped, silky-hirsute outside, sericeous inside; basal portion narrowly ellipsoid, ellipsoid or ovoid, sericeous outside, glabrous inside. *Sepals* patent, unequal, sericeous on both sides; anterior one at least three times longer than other three, obovate, 8.3–16.3 × 2.3–6.5 mm, apex acute to rounded; lateral ones narrowly elliptic to narrowly obovate, 2.0–5.5 × 0.4–1.3 mm, apex acute to rounded; posterior one narrowly elliptic to elliptic or narrowly ovate, 2–4 × 0.5–1.3 mm, apex acute to rounded. *Stamens* exserted; outer, antesepalous whorl arising near base to $^1/_5$ way up sepal; inner, antepetalous whorl arising at rim of hypanthium; outer filaments 0.6–2.5 mm long, inner 0.7–2.0 mm long; anthers ellipsoid to subrotund, 0.4–0.8 mm long, abaxially without broad connective tisssue. *Floral scales* exserted, arising in mouth of hypanthium immediately below antepetalous stamens, obovoid, 0.4–0.7 mm long, glabrous, yellow in fresh state. *Ovary* narrowly obovoid to ovoid, 1.8–3.0 mm long, attenuate at base, sericeous throughout or only near apex. *Style* filiform, upper $^1/_3$–$^1/_2$ covered with ascending hairs, glabrous below. *Stigma* brush-like (Figure 33).

Distribution and ecology

Lachnaea macrantha has been recorded from the Slanghoek to Riviersonderend Mountains in the southwestern part of Western Cape and from the Langeberg Mountains in the Swellendam and Riversdale Districts.

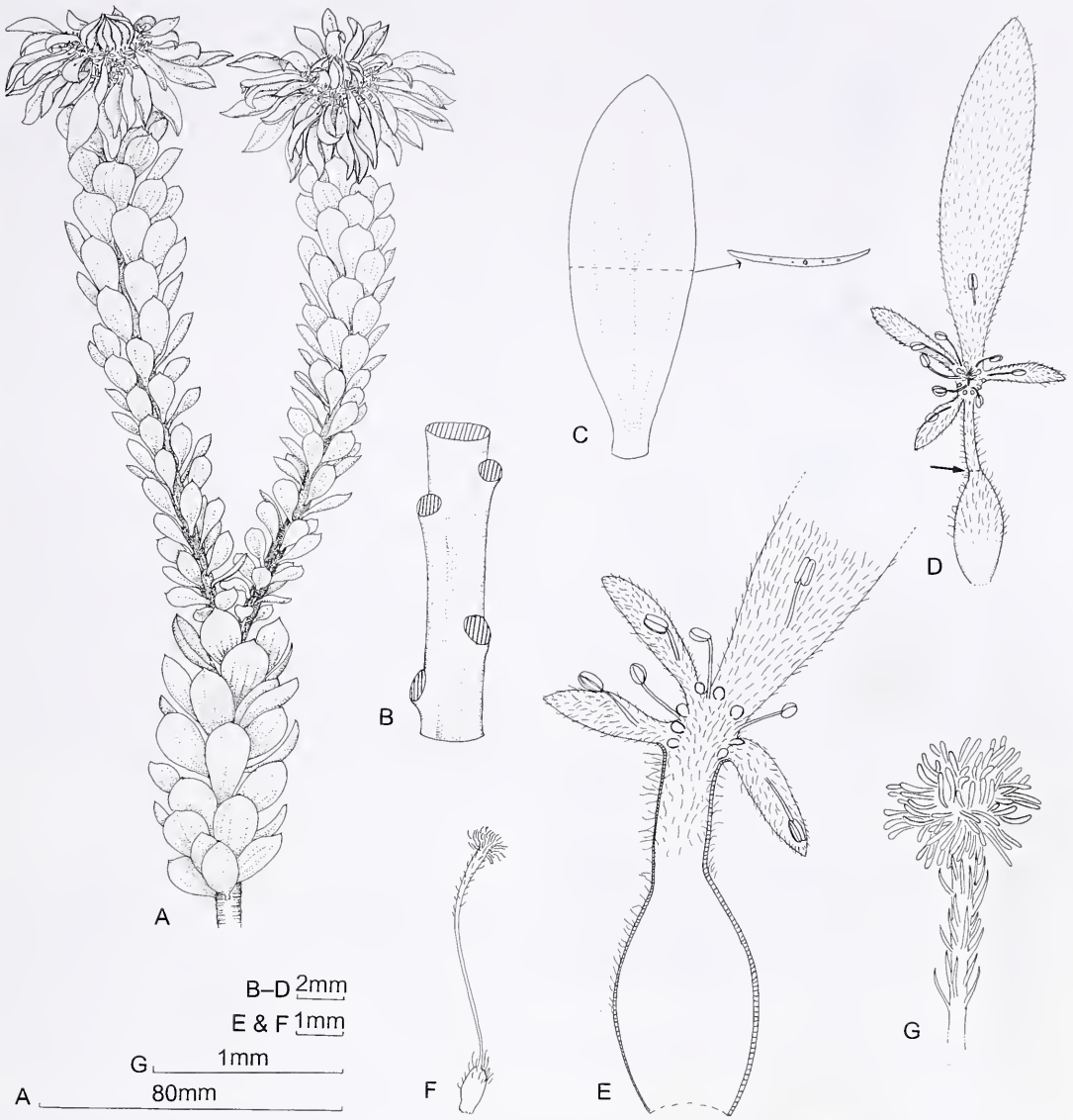

FIGURE 33.—*Lachnaea macrantha*, *I. Oliver 3* (NBG). A, portion of plant; B, branch with leaves removed; C, leaf, abaxial view and c/s. D, E, flower: D, circumscission zone arrowed; E, l/s with gynoecium removed. F, gynoecium; G, stigma and upper portion of style. Scale bars: A, 80 mm; B–D, 2 mm; E–G, 1 mm.

It is a montane species with a localized distribution, occurring amongst rocks and in rock crevices on the southern, southeastern or western mountain slopes at altitudes between 1 330 and 2 255 m (Figure 34). *Flowering time*: September to January and April.

Conservation status: Lower Risk Least Concern (LRlc). Although this species has a wide distribution, it is vulnerable to frequent fires. Due to frequent fires it has apparently disappeared locally from the southern slopes of Jonaskop, 3319 (Worcester) DC, where it was last collected in 1970.

Diagnostic characters and relationships

Lachnaea macrantha and *L. pomposa* both have capitate, pedunculate inflorescences. *L. macrantha* is distinguished from *L. pomposa* by being a reseeder, with daisy-like not pompom-like inflorescences, a large anterior sepal, which is at least three times the length of the other three, and with epistomatic leaves.

Vouchers: *Esterhuysen 11163* (BOL, NBG, PRE); *Forsyth 527* (K, NBG, NY, PRE); *McDonald 1552* (NBG); *Oliver 3195* (NBG), *11017* (NBG); *I. Oliver 3* (NBG, PRE). Total number of specimens examined: 52.

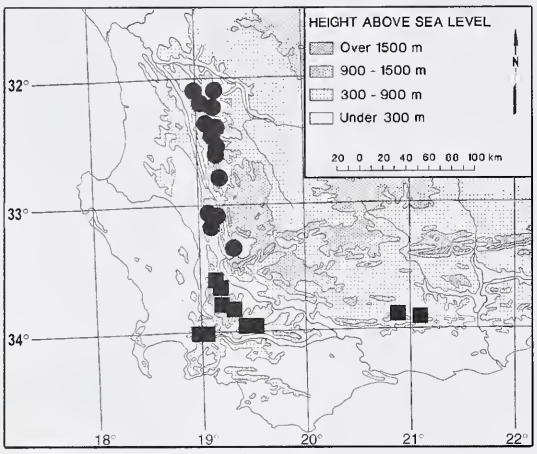

FIGURE 34.—Known distribution of *Lachnaea macrantha*, ■; and *L. filamentosa*, ●.

13. **Lachnaea filamentosa** *Meisn.* in Linnaea 14: 410 (1840); Meisn.: 575 (1857); C.H.Wright: 20 (1915). Type: Cederberg near Honigvalei [Heuningvlei], alt. 3000–3500 ft (III. A. d.), *Drège s.n.* (NY, holo.!–two collections on sheet: *Burchell 7120* [= *L. macrantha*] and the other specimen on the right with a capsule, annotated by Meisner as '*Gnidia filamentosa* Th.', *Drège 12*; K!, P!, S!, iso.).

Gnidia filamentosa Thunb.: 76 (1794); Thunb.: 378 (1823) p.p., non L.f. Type: Caput Bonae Spei (UPS, *Thunberg sheet 9550* –NBG, photocopy!).

Note: two specimens in herb. Thunberg are annotated by Thunberg as *Gnidia filamentosa 1* and *Gnidia filamentosa 2* respectively. He assumed that these two specimens were conspecific with *G. filamentosa* L.f. However, in his description of the species (Thunberg 1823) he mentions that the sepals are unequal, which distinguishes it from *G. filamentosa* L.f. *G. filamentosa 1* is *L. filamentosa Meisn.* and *G. filamentosa 2*, with its regular sepals, is *L. pomposa*.

Lachnaea filamentosa Meisn. var. *major* Meisn.: 575 (1857); C.H.Wright: 20 (1915). Type: Winterhoeksberg near Tulbagh, mountain slopes, alt. 5, *Ecklon & Zeyher 72* (?S, holo.! –without coll. no. but annotated by Meisner; NBG!, Z!, ?iso.).

Erect, sparsely to moderately branched shrub up to 2 m tall, single-stemmed or multistemmed at base; reseeder or resprouter. *Branches* ascending, semi-rigid to rigid, terete or ridged below leaf bases, glabrous, leafy, becoming naked with prominent leaf scars. *Leaves* alternate, ascending, imbricate or patent with tips turned upward, closely set, sessile, amphistomatic, glabrous, 7–40 × 2–13 mm, narrowly elliptic to elliptic, narrowly obovate to obovate, narrowly ovate or occasionally ovate, coriaceous, flat, glaucous or dull green, sometimes those below inflorescence tinged blue; adaxially enervate, dull, ± white-punctulate; abaxially enervate or faintly nerved, glossy, occasionally ± white-punctulate; apex subacute, acute or mucronulate; base cuneate, occasionally attenuate. *Inflorescence* a terminal, ebracteate capitulum, usually more than 50-flowered with 10 to more than 50 open flowers at a time, 30–100 mm diam., basally enclosed by foliage leaves, pedunculate; peduncle 1–15 mm long, sericeous. *Receptacle* narrowly conical to conical, 5–25 × 2–11 mm, puberulent. *Flowers* sessile, zygomorphic, blue, lilac-blue, cream or cream with a lilac or blue flush, fragrantly scented. *Hypanthium* 6.3–17.5 mm long, circumscissile ± $^1/_5$–$^1/_3$ from base; upper portion narrowly funnel-shaped, covered with long, ascending to patent, silky hairs admixed with shorter adpressed, crooked hairs on outside, inside densely adpressed hairy, glabrescent towards circumscission zone; basal portion ellipsoid to ovoid, sericeous outside, glabrous inside. *Sepals* patent, sericeous on both sides, unequal, anterior one almost twice to three times as long as other three, narrowly elliptic to elliptic or narrowly obovate, 6.5–30.0 × 2.0–10.6 mm, apex acute to rounded; lateral ones narrowly elliptic to elliptic or narrowly obovate, 3.5–10.5 × 1.0–2.8 mm, apex acute to rounded; posterior one narrowly ovate to narrowly obovate or ovate to elliptic, 3.3–8.0 × 1.0–2.5 mm, apex acute to rounded. *Stamens* exserted; outer, antesepalous whorl arising on sepals [anterior one arising at base to a $^1/_3$ way up, other three arising near base]; inner, antepetalous whorl arising at rim of hypanthium; filaments 1.0–5.3 mm long; anthers ellipsoid to broadly oblong, 0.6–1.5 mm long. *Floral scales* exserted, arising at mouth of hypanthium immediately below antepetalous stamens, narrowly obovoid to obovoid or narrowly ovoid, 0.3–1.0 mm long, with stiff hairs at apex, yellow in fresh state. *Ovary* ellipsoid to obovoid, 1.4–5.0 mm long, tufted at apex, also occasionally adpressed hairy along side below style attachment. *Style* linear, 6.2–15.6 mm long, silky pubescent in upper $^1/_3$–$^1/_2$, lower portion glabrous. *Stigma* brush-like (Figure 35).

Distribution and ecology

Lachnaea filamentosa is restricted to Western Cape, ranging from the Pakhuis Mountains in the Clanwilliam District in the north along the Cederberg range southwards through the Groot Winterhoek and Roodesand Mountains near Tulbagh to Mostertshoek Mountain near Ceres (Figure 34). It occurs on stony, rocky soil or rocky outcrops, sandy areas along streamsides, or in seasonally damp areas at altitudes between 665 and 1 900 m.

There is considerable variation in the size of plants as well as in leaf, inflorescence and flower size. Those from the Groot Winterhoek and Roodesand Mountains, growing in seepage areas at altitudes between 1 000 and 1 665 m are the most robust. Throughout the range individuals growing in moist areas seem to be more luxuriant than those on open, sandy, drier areas. One collection (*Levyns 2205*) from Grootlands Peak in the Cederberg has exceptionally narrow leaves and sepals. *Flowering time*: July to February, with a peak from August to December.

Conservation status: Lower Risk Least Concern (LRlc).

Diagnostic characters and relationships

Lachnaea filamentosa, *L. macrantha* and *L. pomposa* belong to the group of species with capitate, peduncu-

late inflorescences. *L. filamentosa* is easily distinguished from *L. pomposa* by the unequal sepals, and from *L. macrantha* by the amphistomatic leaves.

Vouchers: *Beyers 110* (NBG, PRE), *245* (K, NBG, PRE); *Dahlgren & Peterson 895* (NBG); *Forsyth 89* (NBG, PRE); *Hansford 47* (NBG, PRE); *Spreeth 146* (NBG, PRE). Total number of specimens examined: 136.

14. **Lachnaea pomposa** *Beyers*, nom. nov.

Gnidia filamentosa L.f., Supplementum plantarum: 224. (1782) [non *Lachnaea filamentosa* Meisn.: 410 (1840)]; Thunb.: 76 (1794); Willd. 2: 425 (1799); Wikstr.: 311 (1818); Thunb.: 328 (1823) [but not the description which agrees with *L. filamentosa* Meisn.]. Spreng.: 239 (1825). *L. buxifolia* Lam.: 373, t. 292, fig. 1 (1792) nom. superfl.: Andrews: 8, t. 524 (1808); Meisn.: 410 (1840); Meisn.: 575 (1857);

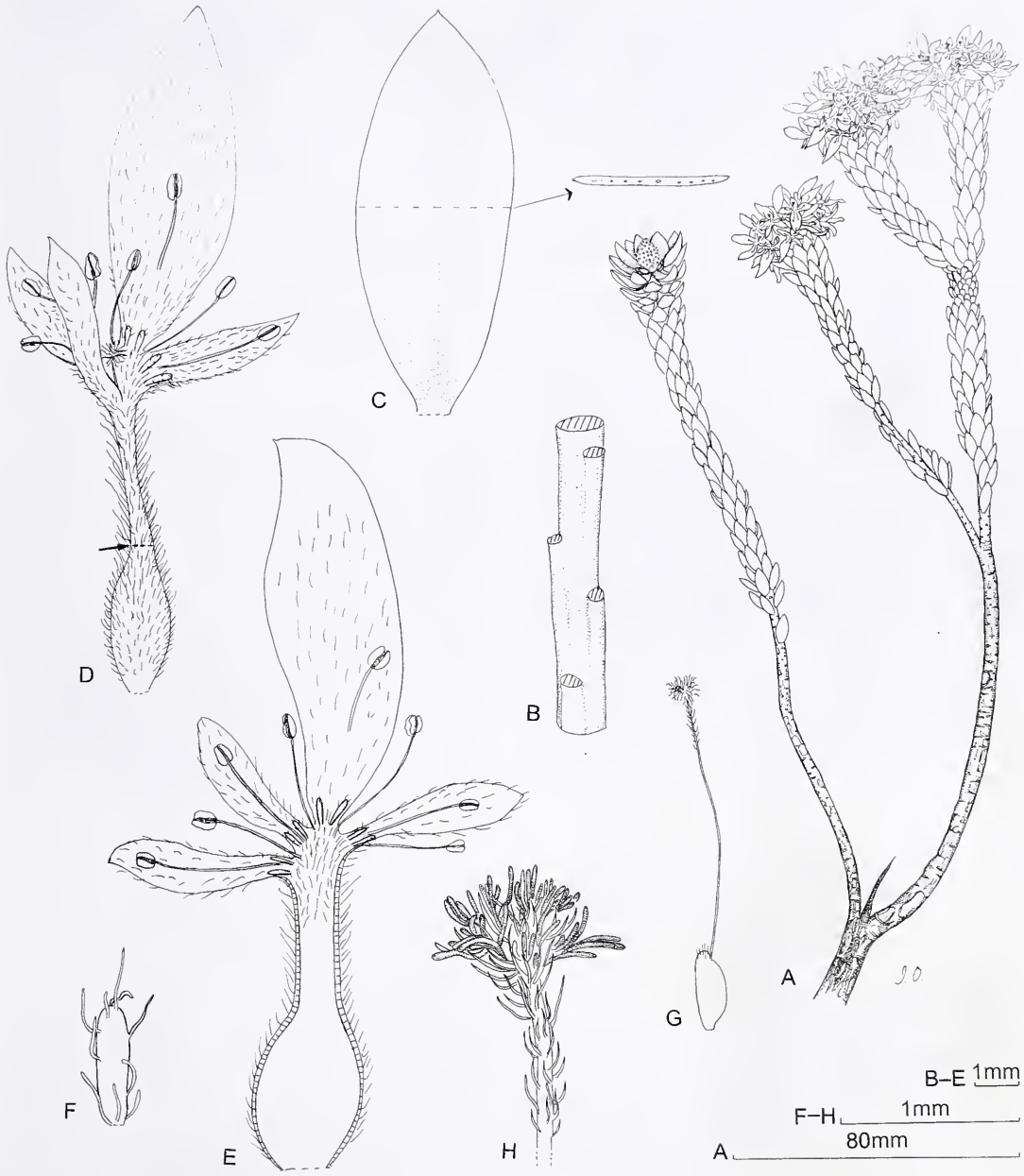

FIGURE 35.—*Lachnaea filamentosa*, *Beyers 110* (NBG). A, portion of plant; B, branch with leaves removed; C, leaf, abaxial view and c/s. D, E, flower: D, circumscission zone arrowed; E, l/s with gynoecium removed. F, scale; G, gynoecium; H, stigma and upper portion of style. Scale bars: A, 80 mm; B–H, 1 mm.

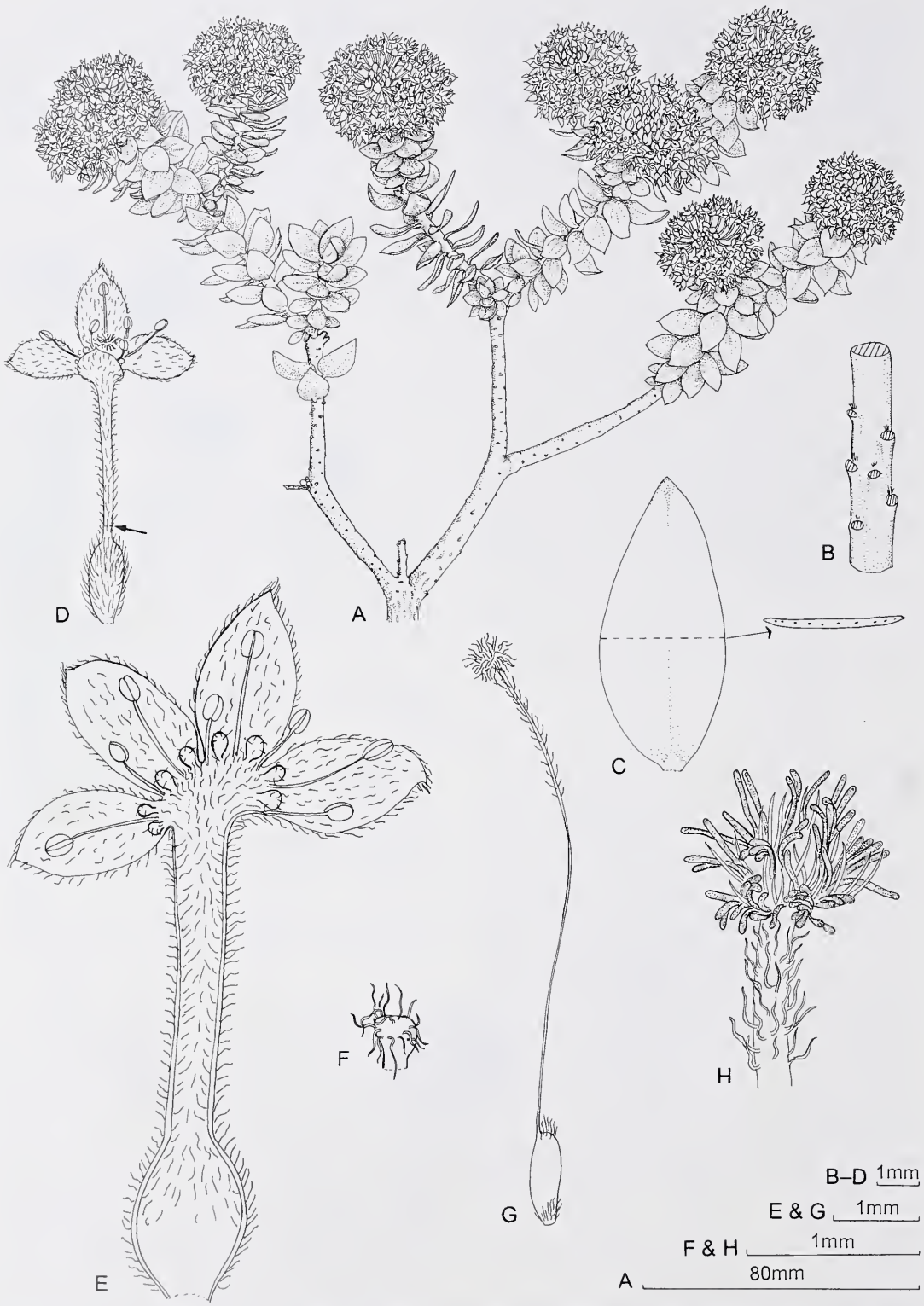

FIGURE 36.—*Lachnaea pomposa*, *Beyers 118* (NBG). A, portion of plant; B, branch with leaves removed; C, leaf, abaxial view and c/s. D, E, flower: D, circumscission zone arrowed; E, l/s with gynoecium removed. F, scale; G, gynoecium; H, stigma and upper portion of style. Scale bars: A, 80 mm; B–H, 1 mm.

C.H.Wright: 19 (1915). *L. glauca* Salisb.: t. 109 (1808) nom. superfl.; W.T.Aiton: 415 (1811); *L. buxifolia* var. *glauca* Sims: t. 1658 (1814b); *G. filamentosa* var. *glauca* Wikstr.: 311 (1818). *L. buxifolia* var. *virens* Sims: t. 1657 (1814a) nom. superfl.; *G. filamentosa* var. *virens* Wikstr.: 311 (1818). *L. filamentosa* (L.f.) Gilg: 240 (1894) nom. illeg. Type: Cape of Good Hope, herb. LINN 502.13 (LINN, lecto., here designated, –PRE, microfiche!, –NBG, photocopy!).

Gnidia grandis hort., ex Sims: t. 1658 (1814b).

Linnaeus filius (1782) was the first to describe this species as *Gnidia filamentosa*. Lamarck (1792) transferred *G. filamentosa* to *Lachnaea* but unfortunately did not take up Linnaeus' epithet and called it *L. buxifolia*. Subsequent authors followed suit and as a result, all the names for this species are illegitimate. Meisner (1840) decided that what Thunberg (1823) had described as *Gnidia filamentosa* was not the same as *G. filamentosa* L.f. He cited *L. buxifolia* Lam. with *G. filamentosa* L.f. non Thunb. in synonymy and described a new plant *L. filamentosa* nob.[Thunb.] with *G. filamentosa* Thunb. in synonymy. With the epithet, *filamentosa,* thus occupied in *Lachnaea*, the new combination by Gilg, *L. filamentosa* (L.f.) Gilg is illegitimate. As all the available names for this species are illegitimate, a new name, *L. pomposa*, is proposed.

Erect, moderately branched shrub up to 1.7 m tall, single-stemmed or multistemmed at base; reseeder or resprouter. *Branches* ascending, stout, rigid, ridged below leaf bases, usually glabrous but occasionally sparsely adpressed hairy towards apex (specimens from Touwsberg), leafy, becoming naked with prominent leaf scars. *Leaves* alternate, ascending to patent, occasionally reclined, those below inflorescences patent to reclined with their tips turned upwards, imbricate, sessile, amphistomatic, glabrous, narrowly elliptic to elliptic, narrowly ovate to widely ovate or narrowly obovate to obovate, 7–38 × 2–19 mm, coriaceous, glaucous; adaxially flat, midveined or subnervate; abaxially flat, faintly nervate; apex mucronulate, obtuse, rounded or acute; base rounded, cuneate or attenuate. *Inflorescence* a terminal, more than 50-flowered, ebracteate capitulum, 25–55 mm diam., basally enclosed by foliage leaves, pedunculate; peduncle 1–10 mm long, shortly sericeous. *Receptacle* subconical to conical, 4–12 × 2.8–6.0 mm, puberulent. *Flowers* sessile, subactinomorphic, cream, occasionally with blueish tint, sweet-scented. *Hypanthium* 9–20 mm long, circumscissile $^1/_5$–$^1/_3$ from base; upper portion narrowly funnel-shaped, silky hirsute or hirsute-tomentose outside, inside densely hairy at mouth, rest adpressed hairy; basal portion ellipsoid, ovoid or obovoid, sericeous or silky hirsute outside, glabrous inside. *Sepals* patent, ± equal, adaxially and abaxially sericeous, ovate or elliptic, 3.5–9.0 × 1.6–5.3 mm, apex acute. *Stamens* exserted; outer, antesepalous whorl arising at base of sepals, usually the longest; inner, antepetalous whorl arising at rim of hypanthium; filaments 1.3–5.0 mm long; anthers ellipsoid to spheroid, 0.4–1.5 mm long. *Floral scales* exserted, arising at mouth of hypanthium immediately below antepetalous stamens, obscured by dense hairs in mouth, narrowly obovoid to obovoid or ellipsoid, 0.4–0.9 mm long, hirsute at apex, occasionally glabrous (specimens from Matroosberg), at first yellow later translucent in fresh state. *Ovary* ellipsoid, 1.4–3.0(–5.0) mm long, tufted at apex, occasionally sericeous in upper half. *Style* filiform, 8.3–18.2 mm long, $^1/_2$ to upper $^1/_4$ adpressed hairy, lower portion glabrous. *Stigma* brush-like (Figure 36).

Distribution and ecology

Lachnaea pomposa is endemic to Western Cape, occurring on the mountain slopes from the Olifants River Mountains in the north through to the Du Toits Mountains in the south, and to the Witteberg and the mountains of the western end of the Little Karoo as far east as the Klein Swartberg at altitudes between 500 and 2 330 m (Figure 37). *Flowering time*: August to January.

Conservation status: Lower Risk Least Concern (LRlc).

Etymology

The specific epithet, derived from *pomposus*, meaning showy or splendid, refers to the showy, pompom-like inflorescences.

Diagnostic characters and relationships

This species, with its more or less regular sepals, can easily be distinguished from *Lachnaea filamentosa* and *L. macrantha* with similar, large, showy, ebracteate capitula but strongly zygomorphic flowers.

Vouchers: *Beyers 118* (K, NBG, PRE), *122* (K, MO, NBG, PRE, NY, Z); *Compton 11962* (NBG); *Esterhuysen 14928* (BOL, NBG); *McDonald 1687* (K, NBG, PRE), *2318* (NBG, PRE). Total number of specimens examined: 101.

15. **Lachnaea capitata** *(L.) Crantz,* Institutiones rei herbariae 1: 129 (1766); Meisn.: 414 (1840) [as var. *pauciflora*]; Meisn.: 552 (1843); Meisn.: 577 (1857) [as var. *pauciflora*]; C.H.Wright: 22 (1915); Levyns: 601

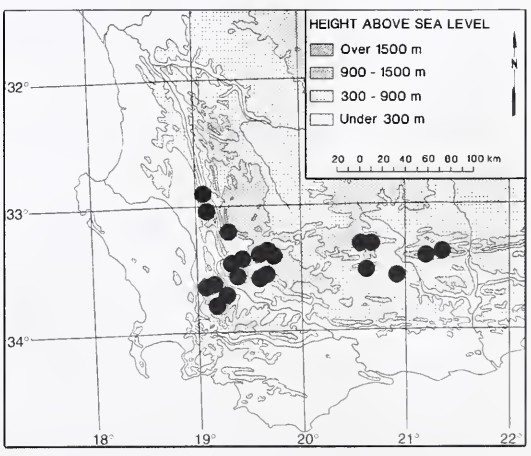

FIGURE 37.—Known distribution of *Lachnaea pomposa*.

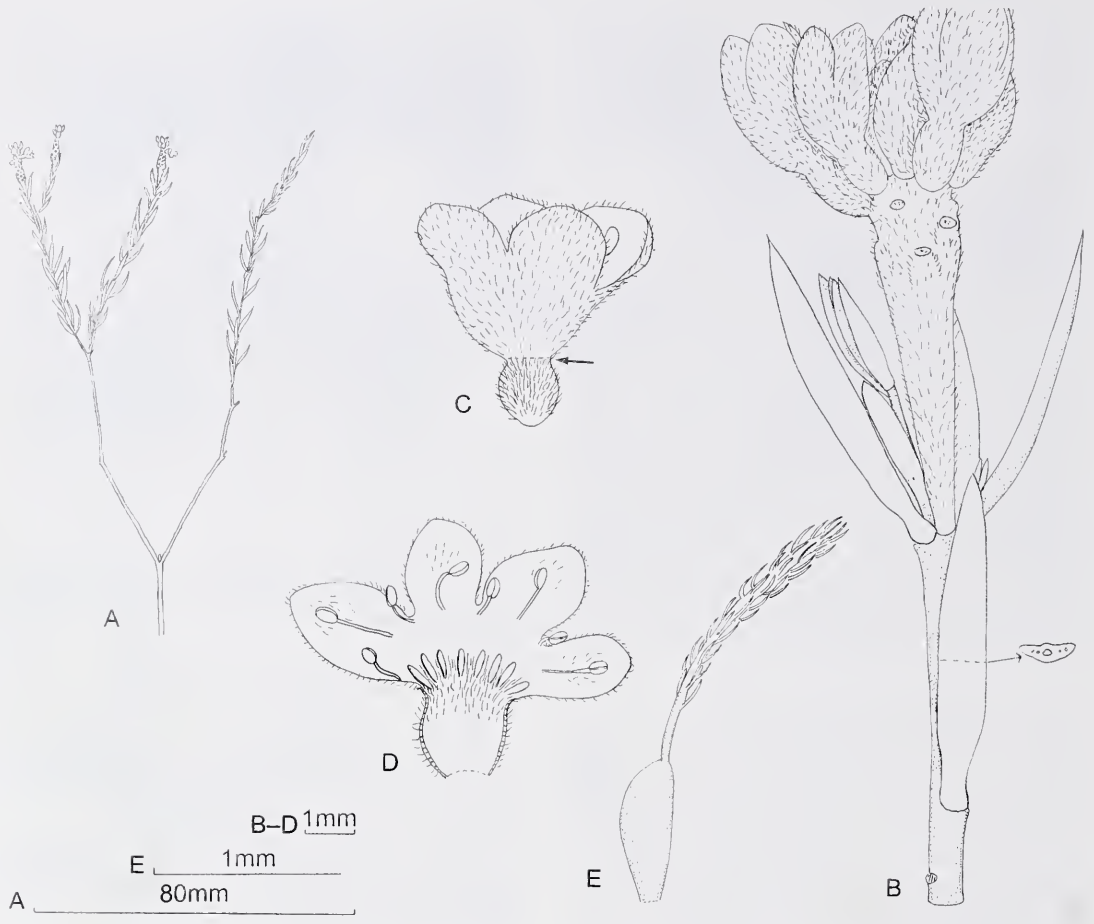

FIGURE 38.—*Lachnaea capitata*, *Beyers 138* (NBG). A, portion of plant; B, flowering branch with leaves and c/s leaf. C, D, flower: C, circumscission zone arrowed; D, l/s with gynoecium removed. E, gynoecium. Scale bars: A, 80 mm; B–E, 1 mm.

(1950); Mason: 150, t. 64, f. 7 (1972). Type: icon (t. 48, fig. 3) in Burman, Rariorum africanarum plantarum (1739), lecto., here designated.

Passerina capitata L.: 88 (1760); L.: 513 (1762); L.: 88 (1764); Burm.f.: 12 (1768); Thunb.: 75 (1794); Wendl.: 18, t. 2, f. 17 (1798); Poir.: 41, t. 291, f. 3 (1804); Wikstr.: 329 (1818); Thunb.: 376 (1823); Spreng.: 240 (1825).

Lachnaea phylicoides Lam.: 374, non t. 392, f. 3 (1792); Meisn.: 414 (1840). Type: [no collector, no date] Herb. Lamarck 19.3-1 (P-LA, lecto., here designated, –NBG, photo.!).

Lachnaea capitata var. *multiflora* Meisn.: 414 (1840); Meisn.: 578 (1857). Type: near Dieprivier, alt. below 100 ft *Drège s.n.* (NY ['Pas. capitata. L. c.' Drège], holo.!; P!, iso.).

Gonophylla acuminata Eckl. & Zeyh. ex Meisn.: 578 (1857) nom. nud. in synonymy.

Gonophylla capitata Eckl. & Zeyh. ex Meisn.: 578 (1857) nom. nud. in synonymy.

Gonophylla conglomerata Eckl. & Zeyh. (pro parte) ex Meisn.: 578 (1857) nom. nud. in synonymy.

Erect, sparsely to moderately branched shrub up to 1.8 m tall, single-stemmed at base; reseeder. *Branches* ascending, slender, lax, occasionally rigid (few individuals from Cape Peninsula), ridged below leaf bases, internodes $^1/_5$ to 2 × leaf length, glabrous or distal 1–4 internodes below inflorescence sericeous, leafy, becoming nude and marked with leaf scars. *Leaves* alternate, ascending, crowded to distant, sessile, amphistomatic, glabrous, linear to narrowly elliptic, 5.2–21.0 × 0.7–1.8 mm, coriaceous, green, concolourous, enervate, glossy, white-punctulate; adaxially ± flat to concave; abaxially flat to convex, sometimes subkeeled; apex acute to acuminate; base cuneate to attenuate. *Inflorescence* a terminal, ebracteate capitulum, 5–16 mm diam., up to 20-flowered with 1–8 open flowers, pedunculate; peduncle 3–6 mm long, sericeous. *Receptacle* at first hemispherical, later after elongating, cylindrical-conical, 0.9–20.2 × 1.5–6.0 mm, sericeous. *Flowers* sessile, subactinomorphic, cream. *Hypanthium* 2.5–4.6 mm long, circumscissile $^2/_5$–$^3/_5$ from base; upper portion obconical; basal portion ovoid, ellipsoid or obovoid, sericeous outside, inside between plane of circumscission and base of floral scales adpressed hir-

sute, rest glabrous. *Sepals* ascending, subequal, elliptic to oblate or ovate to widely depressed ovate, 1.2–2.8(–5.0) × 1.2–3.2 mm, adaxially densely to sparsely covered with short, silky, adpressed hairs, abaxially sericeous, apex rounded to obtuse. *Stamens* exserted or inner, antepetalous whorl only anthers exserted, outer, antesepalous whorl arising at base of sepals, inner, antepetalous whorl arising a $^1/_4$–$^1/_2$ down upper portion of hypanthium; filaments 0.3–1.7 mm long, inner whorl shorter than outer whorl; anthers ellipsoid to spheroid, 0.4–0.7 mm long, abaxially without broad connective tissue. *Floral scales* included, arising $^2/_3$–$^3/_4$ down upper portion of hypanthium, narrowly oblong, 0.4–0.9 mm long, glabrous, translucent or yellow-translucent. *Ovary* ellipsoid to obovoid, 0.7–1.6 mm long, glabrous. *Style* filiform, 1.7–4.7 mm long, adpressed hairy to sparsely adpressed hairy. *Stigma* brush-like (Figure 38).

Distribution and ecology

Lachnaea capitata is restricted to Western Cape, where it occurs on sandy flats and lower mountain slopes from Clanwilliam in the north, southwards to the Cape Peninsula and inland to Franschhoek and Goudini (Figure 39). *Flowering time*: June to March.

Conservation status: Vulnerable (VU A1c). *L. capitata* may have disappeared from the Cape Peninsula as a result of urban development, as no recent collections have been made. Very few recent collections are known from the sandy flats up the west coast and in the Tygerberg area.

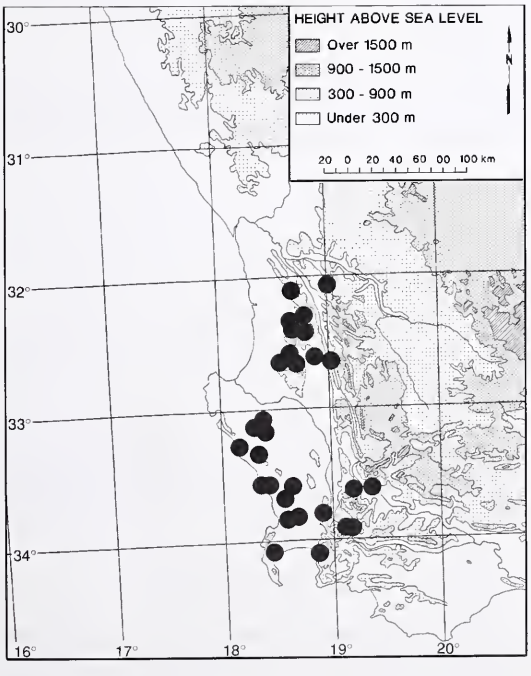

FIGURE 39.—Known distribution of *Lachnaea capitata*.

Diagnostic characters and relationships

Lachnaea capitata is a sister species of *L. densiflora* based on the following shared characters: leaves abaxially convex, upper portion of hypanthium not stalked and floral scales arising below midway on upper portion of hypanthium. It can, however, be distinguished from *L. densiflora* by the usually glabrous branches (sericeous or sericeous-tomentose branches), the inflorescence with 1–8 open flowers (up to 20 open flowers) and the ascending sepals with sericeous indument (patent sepals with tomentose indument).

Vouchers: *Bean & Viviers 2054* (BOL, NBG, PRE); *Beyers 138* (K, NBG, PRE); *Bolus 12820* (BOL, GRA, PRE, Z); *Dahlgren & Peterson 374* (NBG); *Oliver 10519* (K, NBG, PRE); *Schlechter 8508* (BOL, GRA, K, PRE, S, Z). Total number of specimens examined: 159.

16. **Lachnaea densiflora** *Meisn.* in DC., Prodromus systematis naturalis regni vegetabilis 14: 578 (1857); C.H.Wright: 22 (1915); Levyns: 601 (1950). Syntypes: 'In planitie Capensi et distr. Caledon', *Ecklon s.n.* [NY (capsule annotated as '*L. capitata* a E. & Z.', marked #, on Meisner Herbarium sheet with different collections of *L. densiflora*)!, lecto., here designated; S!(locality on sheet in Meisner's handwriting, but unfortunately he did not write the species name on the sheet), isolecto.], *Ludwig* (not seen), *Niven* (not seen), *Zeyher 1483* (BOL!, K!, PRE!, S!, SAM!, Z!).

Note: Zeyher 1483, which is well represented in the different herbaria, could not be chosen as there was no indication whether Meisner had seen any of the sheets.

Erect, corymbosely, moderate to much-branched shrub up to 0.5 m tall, single-stemmed at base; reseeder. *Branches* ascending, semi-rigid, ridged below leaf bases, sericeous or sericeo-tomentose, densely leafy, the older sparsely hairy or glabrous and naked with prominent leaf scars. *Leaves* alternate, ascending to inclined, below inflorescence often patent with apex turned upward, crowded to distant, internodes $^1/_5$ to as long as leaf length, sessile, amphistomatic, glabrous or occasionally margins ciliate or apex tufted, later becoming glabrous, linear to narrowly elliptic, 5–12(–20) × 0.7–2.5 mm, coriaceous or slightly fleshy, green, concolorous, enervate, glossy or dull, white-punctulate, in dried state longitudinally wrinkled; adaxially ± flat to concave; abaxially convex, sometimes subkeeled; apex acuminate, occasionally acute; base cuneate to attenuate. *Inflorescence* a terminal, ebracteate capitulum, globose, 8–16 mm diam., ± 40-flowered with up to 22 open flowers, pedunculate; peduncle 5–10 mm long, sericeous or tomentose-sericeous. *Receptacle* at first hemispherical, later, after elongating, conical to widely conical, 2–8 × 3.4–7.5 mm, sericeous. *Flowers* sessile, subactinomorphic, cream, cream with a pink flush, or pale to dark pink. *Hypanthium* 1.7–3.9 mm long, circumscissile $^3/_5$–$^3/_4$ from base; upper portion widely obconical; basal portion ovoid or ellipsoid, sericeous to villosulous outside, inside adpressed hirsute between base of floral scales and plane of circumscission, rest glabrous. *Sepals* patent, subequal, ovate to widely depressed ovate, 1.7–3.5

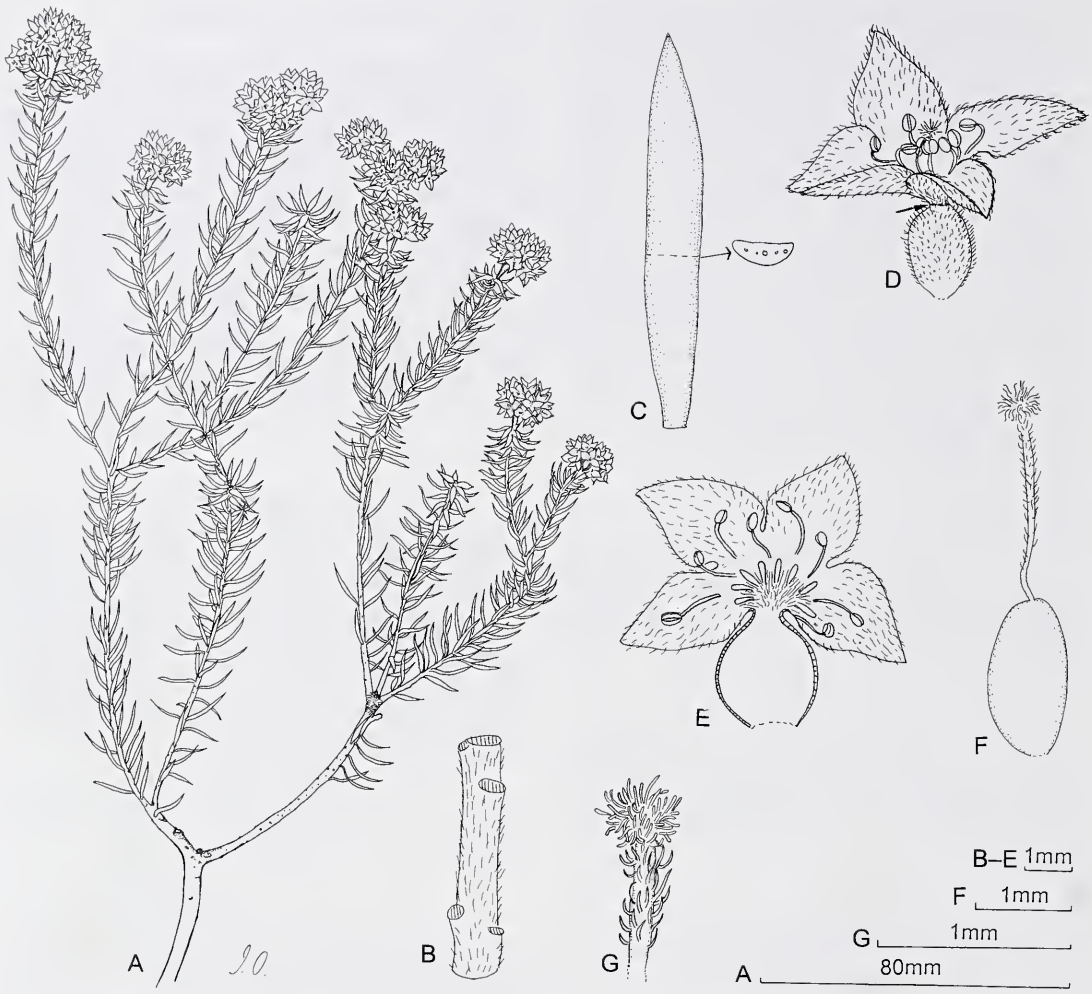

FIGURE 40.—*Lachnaea densiflora*, *Oliver 9129* (NBG). A, portion of plant; B, branch with leaves removed; C, leaf, abaxial view and c/s. D, E, flower; D, circumscission zone arrowed; E, l/s with gynoecium removed. F, gynoecium; G, stigma and upper portion of style. Scale bars: A, 80 mm; B–G, 1 mm.

× 1.2–3.1 mm, adaxially tomentose, abaxially tomentose or occasionally sericeo-tomentose, apex rounded to obtuse. *Stamens* exserted; outer, antesepalous whorl arising at base of sepals; inner, antepetalous whorl arising $^1/_4$–$^1/_3$ down upper portion of hypanthium; filaments 0.5–1.8 mm long, inner whorl shorter than outer whorl; anthers ellipsoid to depressed spheroid, 0.3–0.4 mm long, abaxially without broad connective tissue. *Floral scales* exserted, arising $^1/_2$–$^2/_3$ down upper portion of hypanthium, linear, 0.5–1.0 mm long, glabrous, yellow in fresh state. *Ovary* ellipsoid to obovoid, 0.7–1.5 mm long, glabrous. *Style* filiform, 1.8–3.1 mm long, adpressed hairy in upper $^1/_2$–$^2/_3$. *Stigma* brush-like (Figure 40).

Distribution and ecology

Lachnaea densiflora is restricted to Western Cape, extending from the southern parts of the Cape Peninsula eastwards to Bredasdorp. It is predominantly a coastal species but has been recorded to occur on sandy flats at low elevations on the Peninsula and along the Palmiet River and in the Klein River Mountains (Figure 41). The explanation regarding the distribution of *L. axillaris* (no. 6) is applicable to that of *L. densiflora*. *Flowering time*: August to March.

Conservation status: Vulnerable (VU A1c). The populations occurring between Rooi Els and Bredasdorp are threatened by the development of residential erven of the coastal towns in the area.

Diagnostic characters and relationships

Lachnaea densiflora is distinguished from *L. capitata*, its sister species, by the sericeous or sericeous-tomentose branches (not usually glabrous branches), the

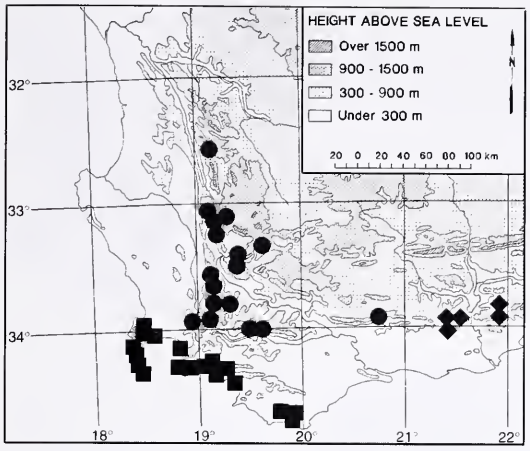

FIGURE 41.—Known distribution of *Lachnaea densiflora*, ■; *L. nervosa*, ●; *L. sociorum*; ◆.

inflorescence with up to 20 open flowers at a time (not with 1–8 open flowers) and the patent, tomentose sepals (not ascending, sericeous sepals).

Vouchers: *Beyers 115* (K, NBG, PRE), *145* (BOL, K, NBG, PRE), *148* (BOL, K, MO, NBG, PRE), *150* (K, MO, NBG, PRE), *154* (K, NBG, PRE), *171* (K, MO, NBG, PRE). Total number of specimens examined: 204.

17. **Lachnaea nervosa** *(Thunb.) Meisn.* in Linnaea 14: 417 (1840); Meisn.: 579 (1857); C.H.Wright: 20 (1915). Type: *Thunberg 9588* (UPS, holo. –NBG, photo.!, –PRE, microfiche!).

Passerina nervosa Thunb.: 75 (1794); Wikstr.:328 (1818); Thunb.: 375 (1823).

Lachnaea ambigua Meisn.: 417 (1840) [as var. *major*]; Meisn.: 576 (1857) [as var. *major*]; C.H.Wright: 23 (1915). Type: Dutoitskloofbergen, alt. 2500–3000 ft, *Drège 7368a* (NY [capsule on *Drège 7378b*], holo.!; P!, iso.!).

Lachnaea ambigua var. *minor* Meisn.: 418 (1840); Meisn.: 577 (1857); C.H.Wright: 24 (1915). Type: Dutoitskloofbergen, in rocky area, alt. 4000 ft., *Drège 7368b* (NY, holo.!; P!–*Drège s.n. b*, iso.).

Gonophylla stricta Eckl. & Zeyh. ex Meisn.: 579 (1857) nom. nud. in synonymy.

Erect, moderately to much-branched shrub up to 0.3 m, rarely up to 1 m tall, single- or multistemmed at base; reseeder or resprouter. *Branches* ascending, occasionally patent, slender to semi-rigid, ridged below leaf bases, internodes up to half as long as leaves, sericeous or sparsely sericeous later glabrescent, leafy, becoming naked with prominent leaf scars. *Leaves* alternate, ascending or patent, close set to scattered, sessile, epistomatic, narrowly elliptic or rarely narrowly obovate, 4.7–14.0 × 0.7–1.5 mm, coriaceous, glabrous; adaxially concave, enervate, dull, faintly white-punctulate; abaxially convex, midribbed or 3–5-ribbed, glossy; apex mucronate or acuminate; base cuneate; distal leaves below inflorescence crowded, green or tinged maroon, may appear bract-like, size variable, those immediately below inflorescence largest, narrowly ovate to obovate, 1.8–9.0 × 1.0–4.2 mm, acuminate or cuspidate, margin glabrous or ciliate. *Inflorescence* a terminal, sessile, ebracteate, 2–14-flowered umbel with 2–5 open flowers at a time, on main and also on short lateral flowering branches below main inflorescence, appearing racemose-like. *Flowers* subactinomorphic, cream or pink, or cream with mauve tinge. *Pedicel* 0.3–2.5 mm long, sericeous. *Hypanthium* 3.5–6.8 (–10.0) mm long, circumscissile a $^1/_3$–$^2/_3$ from base; upper portion funnel-shaped, sericeous on both sides, trichomes acicular; basal portion ovoid or ellipsoid, sericeous outside, trichomes blunt or subacute, glabrous inside. *Sepals* patent, subequal, narrowly ovate to widely elliptic, 2.3–5.2(–8.2) × 1.1–3.0 mm, apex acute to obtuse, adaxially sparsely sericeous or glabrous, abaxially sericeous. *Stamens* exserted; outer, antesepalous whorl arising at base of sepal; inner, antepetalous whorl arising at rim of hypanthium, shorter than outer whorl; outer filaments 1.0–2.4(–4.0) mm long, inner 0.6–1.5(–2.0) mm long; anthers ellipsoid to widely ellipsoid, 0.5–0.9(–1.2) mm long, abaxially without broad connective tissue. *Floral scales* exserted, arising at mouth of hypanthium immediately below antepetalous stamens, linear or narrowly ellipsoid, 0.7–1.7(–2.4) mm long, glabrous, translucent white in fresh state. *Ovary* ellipsoid or rarely obovoid, 0.9–1.9 mm long, glabrous, usually with tuft of hair at style attachment. *Style* linear, 3.0–6.0(–10.5) mm long, covered with straight, silky, ascending hairs throughout or only in upper half. *Stigma* brush-like (Figure 42).

Distribution and ecology

Lachnaea nervosa has been recorded along the mountains from Elandskloof south of Citrusdal in the north to the Jonkershoek Mountains in the Stellenbosch District and eastwards through the Riviersonderend Mountains to the Langeberg near Swellendam (Figure 41). Apart from the Zeyher collection, no other herbarium specimens of this species are known from the Langeberg. It occurs on the upper slopes and summit ridges at altitudes between 830 and 2 000 m. *Flowering time*: July to December.

Meisner regarded *Lachnaea ambigua* as very similar to *L. nervosa*, from which it is distinguished mainly by the shorter branches and the leaves being two to four times shorter. Over its distribution range, variation in growth form and leaf length could be correlated with variation in habitat: on the open slopes in the drier regions the plants are more compact and usually not more than 0.4 m tall. The length of the leaves varies from 4.7 to 12 mm. Plants growing on steep rocky slopes in wetter areas, as in the Du Toit's Kloof and Stellenbosch Mountains, are more slender, upright, and up to 1 m tall, with the leaf length varying from 5 to 14 mm. The variation exhibited encompasses Meisner's concepts of the two species and therefore *L. ambigua*, the more recent name, must be regarded as a synonym of *L. nervosa*.

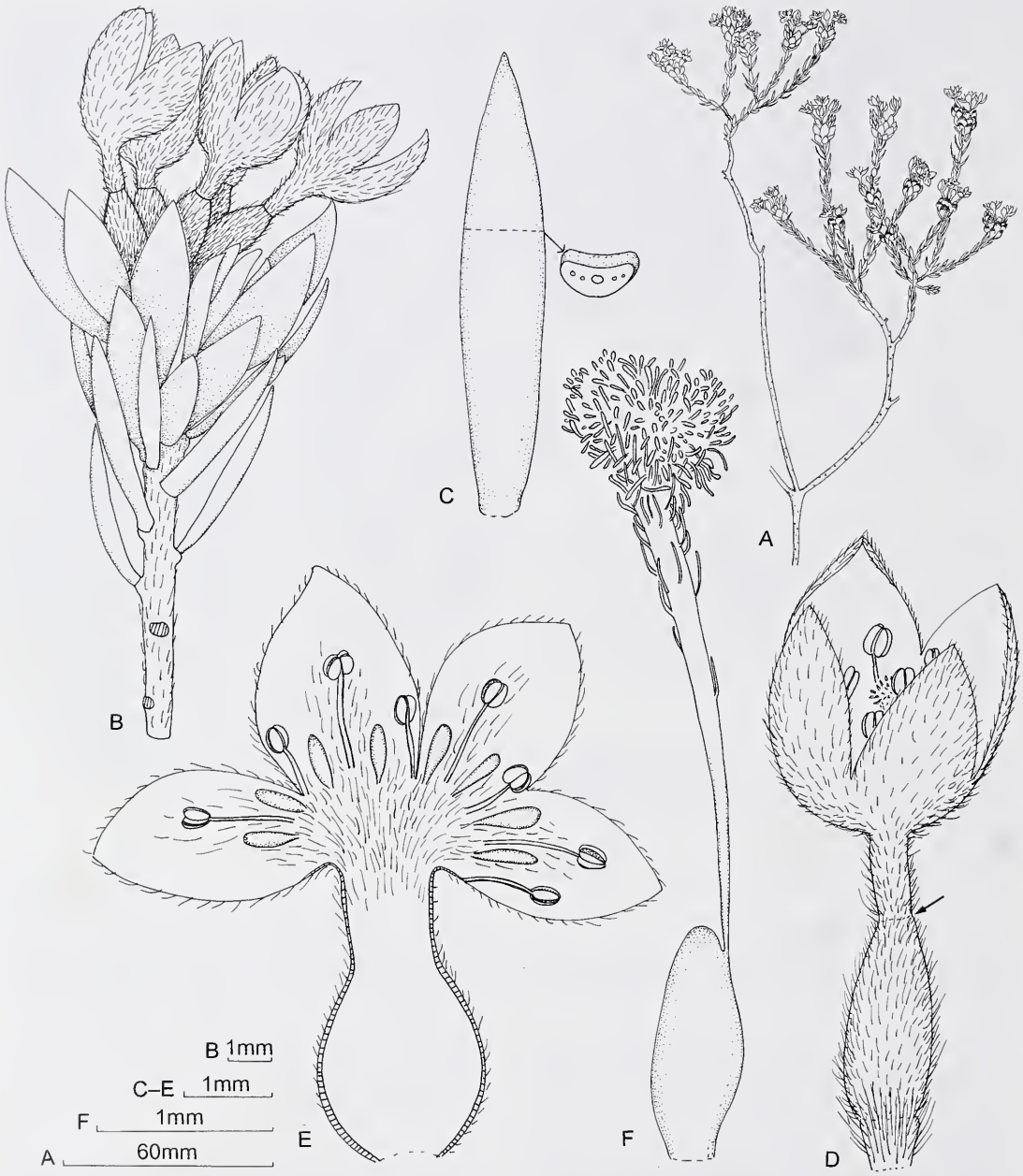

FIGURE 42.—*Lachnaea nervosa*, *Oliver 9259* (NBG). A, portion of plant; B, flowering branch; C, leaf, abaxial view and c/s. D, E, flower: D, circumscission zone arrowed; E, l/s with gynoecium removed. F, gynoecium. Scale bars: A, 60 mm; B–F, 1 mm.

Conservation status: Lower Risk Least Concern (LRlc).

Diagnostic characters and relationships

Lachnaea nervosa can be distinguished from *L. striata*, a species also having ebracteate umbels, alternately arranged leaves and leaves abaxially 1–5-ribbed with crisped ciliate margins, by the eciliate leaves, the basal portion of the hypanthium covered on the outside by silky, blunt to subacute trichomes, and the long, linear or narrowly elliptic floral scales which may be almost as long or longer than the antesepalous stamens.

Vouchers: *Beyers 215* (BOL, K, PRE, NBG); *Boucher 2402* (NBG, PRE); *Esterhuysen 36180* (BOL, NBG); *Oliver 9259* (K, NBG, PRE); *Salter 4699* (BOL, K, PRE, SAM); *Zeyher 3767* (BOL, PRE, S, SAM). Total number of specimens examined: 104.

18. **Lachnaea sociorum** *Beyers* in Beyers & A.E. van Wyk in Bothalia 28: 49 (1998b). Type: Western Cape, 3321 (Ladismith): Langeberg, Bergfontein, S-facing midslopes of Koksposberg, 379 m, (–DC), 18-01-1991, *McDonald 2059* (NBG, holo.!; BOL!, K!, NY!, PRE!, iso.).

Lachnaea diosmoides var. *major* Meisn.: 579 (1857). Type: *Zeyher s.n.* (S, holo.!). Meisner, however, expressed his doubt regarding the status of this variety.

Lachnaea crassifolia Meisn.: 579 (1857) nom. nud.

Calysericos parviflora Eckl. & Zeyh. (ex parte) ex Meisn.: 579 (1857) nom. nud.

Erect, compact, moderately branched shrub up to 0.6 m tall, multistemmed at base; resprouting after fire. *Branches* erect, slender, ridged below leaf bases, covered with long, straight, adpressed hairs admixed with crooked ones, densely leafy, becoming naked with prominent leaf scars. *Leaves* alternate, ascending or occasionally inclined to patent, with apex curled inward, imbricate, sessile, lanceolate to narrowly elliptic or occasionally elliptic to obovate, 3.6–6.0 × 0.9–2.4 mm, coriaceous, green, those below inflorescence sometimes tinged maroon, glabrous; adaxially concave, smooth, dull, ± white-punctulate; abaxially convex, faintly 3-ribbed or towards apex subkeeled, glossy, subpapillate; apex acute; base cuneate. *Inflorescence* a terminal, sessile, ebracteate, 6–14-flowered umbel with up to 9 open flowers at a time, on main flowering branches. *Flowers* subactinomorphic, white, skunk-scented. *Pedicel* 0.3–0.7 mm long, sericeous. *Hypanthium* 2.5–3.7 mm long, circumscissile, $^3/_5$–$^3/_4$ from base; upper portion funnel-shaped, tomentose outside, adpressed hirsute inside; basal portion oblong, glabrous, rarely tomentose outside, glabrous inside. *Sepals* patent, subequal, widely ovate or subrotund, 1.7–3.0 × 1.7–3.2 mm, apex rounded or obtuse, adaxially and abaxially tomentose. *Stamens* exserted; outer, antesepalous whorl arising at base of sepals, 0.7–1.5 mm long; inner, antepetalous whorl arising at rim of hypanthium, 0.5–1.2 mm long (inner stamens the shortest or equal to shortest of outer stamens); anthers widely ellipsoid, 0.4–0.6 mm long, abaxially without broad connective tissue. *Floral scales* exserted, arising at mouth of hypanthium immediately below antepetalous stamens, obovoid or subglobose, 0.3–0.5 mm long, glabrous, translucent-white when fresh. *Ovary* ellipsoid or obovoid, 0.9–1.4 mm long, glabrous. *Style* terete-obconical, 2.0–2.9 mm long, with straight, adpressed or incurled hairs in upper $^1/_2$–$^2/_3$. *Stigma* brush-like (Figure 43).

Distribution, ecology and variation

Recorded from the eastern end of the Langeberg Mountains, from Perdeberg in the west eastwards to Gavelsbos and the southern slopes of the Attakwa Mountains below Perdekop. Plants occur in stony soil on the southern and northern slopes, at altitudes between 300 and 1 100 m (Figure 41). *Flowering time*: August to January.

The population on the northern side of the Langeberg at Tygerberg, west of Huisrivier, is very localized and reasonably old. These plants are single-stemmed at the base, branching close to the ground and are open at the crown with decumbent branches. Whether they would resprout after a fire remains to be seen. Two collections were made from this area, viz. *Beyers 176* and *McDonald 1780*. In all the material collected by McDonald, the basal portion of the hypanthium is glabrous as in all collections from other localities. However, in the material collected by Beyers, the basal portion of the hypanthium on the outside is tomentose like the rest of the flower. This variation in hairiness needs further investigation before it can perhaps be formally expressed taxonomically.

Conservation status: Lower Risk Least Concern (LRlc).

Diagnostic characters and relationships

Lachnaea sociorum is closely related to *L. ericoides* Meisn.; they have a similar inflorescence and floral structure. In both species the lower portion of the hypanthium is glabrous (except for the one collection of *L. sociorum*, *Beyers 176*, where it is tomentose). In *L. sociorum* the leaves are usually lanceolate to narrowly elliptic, abaxially faintly 3-ribbed, with an acute, glabrous apex, the sepals are adaxially tomentose and the stigma penicillate. In *L. ericoides*, on the other hand, the leaves are narrowly elliptic to obovate, abaxially keeled, with a rounded, tufted apex, the sepals are adaxially sericeous-tomentose and the stigma capitate with elongated papillae.

Vouchers: *Beyers 176* (BOL, K, NBG, NY, PRE, Z); *Bolnen 8479* (NBG, PRE); *Haynes 1401* (NBG, PRE); *McDonald 1963* (PRE, NBG) *Oliver 10524* (BOL, NBG, PRE), *10829* (BOL, K, NBG, PRE, S). Total number of specimens examined: 38.

19. **Lachnaea diosmoides** *Meisn.* in Linnaea 14: 418 (1840) [as var. *elatior* on p. 419]; Meisn.: 552 (1843); Meisn.: 578 (1857); C.H.Wright: 23 (1915); Batten & Bokelmann: 109, t. 88, fig. 9 (1966). Syntypes: mountain near Hoogekraalsrivier, below 1000–2000 ft, [19-09-1831], *Drège a* [*Lachnaea phylicoides* Lam. *a*] (K!, P!, PRE!); at margin of mountain forest near George, 1000–1500 ft, [29-08-1831], *Drège b* [*Lachnaea phylicoides* Lam. *b*] (NY!, lecto., here designated; P!, SAM!, isolecto.).

Lachnaea phylicoides Lam.: t. 292, fig. 3 (1792), non: 374 (1792), nec Herb.; Drège: 117, 124 (1843).

Lachnaea diosmoides var. *tenella* Meisn.: 419 (1840); Meisn.: 579 (1857); C.H.Wright: 23 (1915). Type: damp flats near Ataquaskloof, 1000 ft, [25-01-1830], *Drège s.n.* [*7366* on specimen] (NY, holo.!; K!, P!, iso.).

Erect, moderately branched shrub up to 1.5 m tall, single-stemmed at base; reseeder. *Branches* erect to flexuous, slender, ridged below leaf bases, glabrous, leafy, becoming naked with prominent leaf scars. *Leaves* alternate, ascending to patent, occasionally reclined, imbricate but towards inflorescence crowded, sessile, epistomatic, linear-elliptic to narrowly elliptic, 5–10 × 1.0–1.5 mm, coriaceous, glabrous; adaxially flat

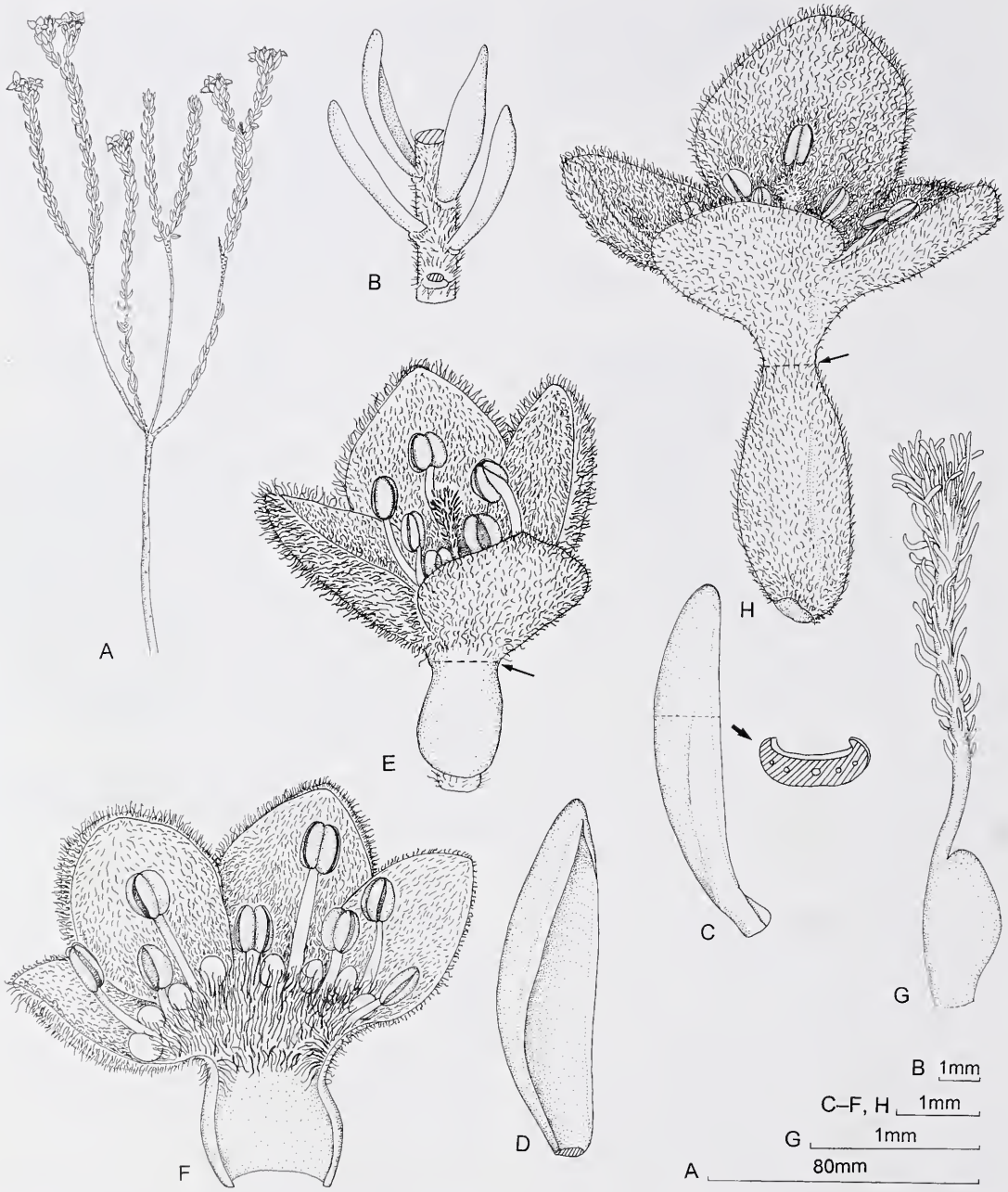

FIGURE 43.—*Lachnaea sociorum*. A, portion of plant; B, branch with leaves. C, D leaves: C, abaxial view and c/s; D, lateral view. E, F, H, flower: E, circumscission zone arrowed; F, l/s with gynoecium removed; H, atypical pubescent form. G, gynoecium. A–G, *McDonald 2059* (NBG); H, *Beyers 176* (NBG). Scale bars: A, 80 mm; B–H, 1 mm.

to obtusely concave, smooth, dull, ± white-punctulate; abaxially obtusely convex, subkeeled in distal $^1/_3$, prominently midribbed, glossy; apex acuminate; base cuneate. *Inflorescence* a terminal, sessile, ebracteate, 6–20-flowered umbel on main and short lateral flowering branches immediately below main inflorescence, which may overtop umbel on main flowering branch, forming a dense cluster of umbels. *Flowers* subactinomorphic to zygomorphic, cream. *Pedicel* 0.2–0.5 mm long, adpressed hirsute. *Hypanthium* 2.0–2.8 mm long, circumscissile $^1/_3$–$^2/_3$ from base; upper portion funnel-shaped, tomentose outside, inside adpressed hirsute between base of floral scales and plane of circumscission, rest tomentose; basal portion oblong, ellipsoid or ovoid, sericeous outside, glabrous inside. *Sepals* ascending, subequal to unequal, posterior one the smallest and

anterior the largest, ovate, elliptic to widely elliptic, obovate or subrotund, 1.4–3.0 × 1.3–2.6 mm, apex rounded or obtuse, both sides tomentose. *Stamens* exserted; outer, antesepalous whorl arising usually at base of sepals, occasionally at rim of hypanthium; inner, antepetalous whorl arising usually at rim of hypanthium, occasionally in mouth of hypanthium; filaments 0.3–1.2 mm long; anthers widely ellipsoid to suborbicular, 0.4–0.8 mm long, abaxially without broad connective tissue. *Floral scales* exserted, arising at mouth of hypanthium immediately below antepetalous stamens, clavate, ovoid or ellipsoid, 0.2–0.7 mm long, glabrous. *Ovary* ellipsoid or ovoid, 0.7–1.0 mm long, glabrous. *Style* linear to linear-obconical, 1.6–2.4 mm long, with straight, adpressed or incurled hairs in upper $^{1}/_{3}$–$^{2}/_{3}$. *Stigma* capitate and papillate (Figure 44).

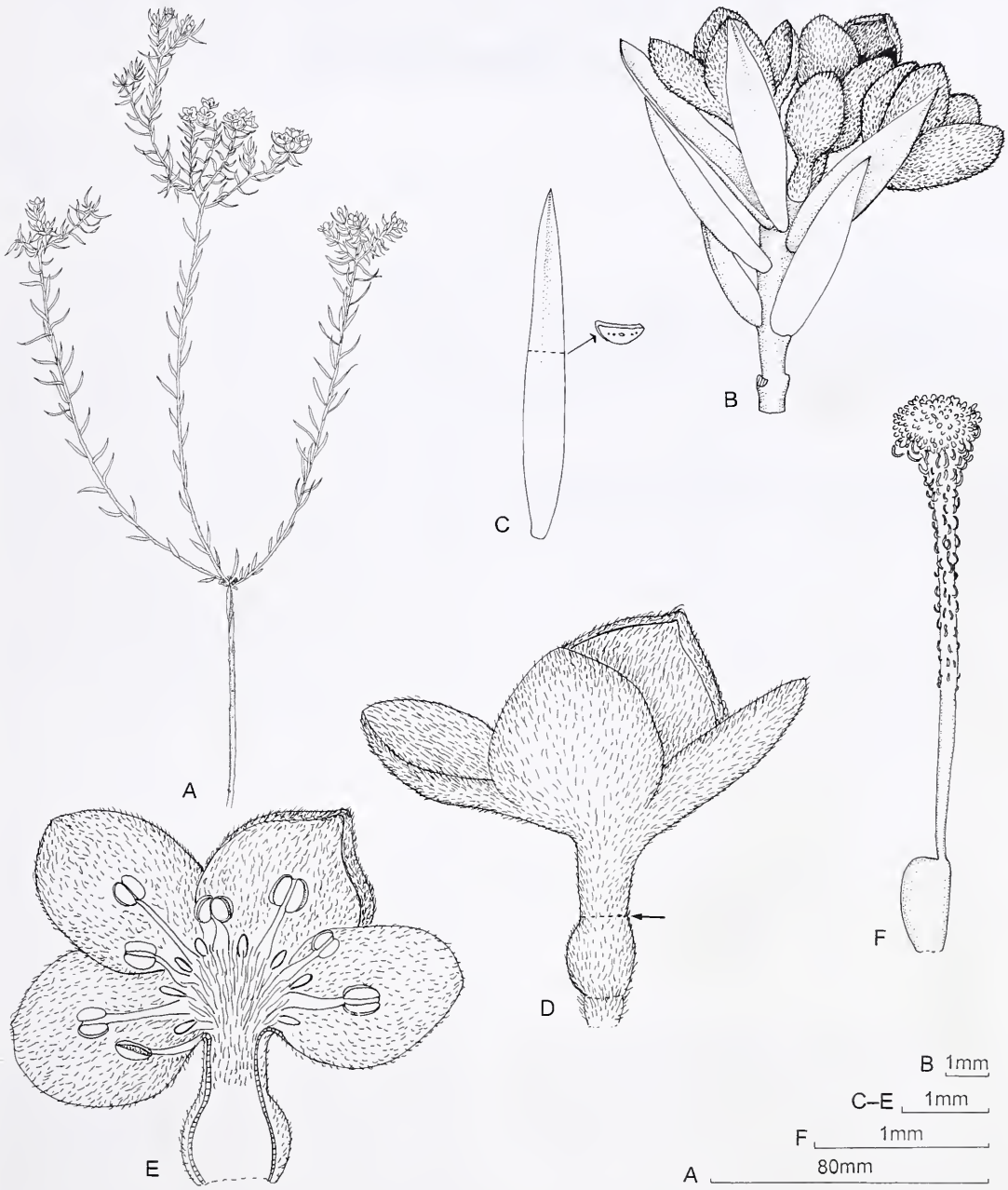

FIGURE 44.—*Lachnaea diosmoides*, *Beyers 181* (NBG). A, portion of plant; B, flowering branch; C, leaf, abaxial view and c/s. D, E, flower: D, circumscission zone arrowed; E, l/s with gynoecium removed. F, gynoecium. Scale bars: A, 80 mm; B–F, 1 mm.

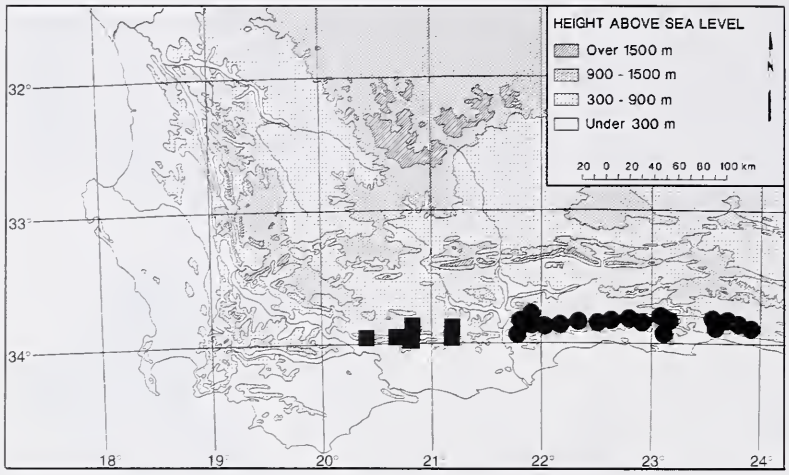

FIGURE 45.—Known distribution of *Lachnaea diosmoides*, ●, and *L. ericoides*, ■.

Distribution and ecology

Lachnaea diosmoides occurs on the slopes of the Attakwas Mountains southwest of Oudtshoorn, across the Outeniqua and Tsitsikamma Mountains, as far east as the Storms River Forest Reserve, at altitudes between 250 and 1 665 m (Figure 45). *Flowering time*: throughout the year.

Conservation status: Lower Risk Least Concern (LRlc). Being a reseeder, frequent fires could impact negatively on this species, moving it into a threatened category very quickly.

Diagnostic characters and relationships

Lachnaea diosmoides is allied to *L. ericoides* and *L. stokoei*. Its erect habit (up to 1.5 m), glabrous leaves and the hypanthium with the basal portion sericeous on the outside, distinguishes it from *L. ericoides* which has a more rounded to straggling habit (up to 0.5 m) and tufted leaves, with the basal portion of the hypanthium glabrous on the outside. It is also easily distinguished from *L. stokoei* in which the floral scales arise abaxially on the hypanthium.

Vouchers: *Beyers 181* (NBG); *Compton 4255* (BOL, NBG); *Dahlgren & Peterson 177* (K, NBG); *Keet 442* (GRA, NBG, PRE); *Schlechter 2337* (BOL, GRA, K, NBG, PRE, Z); *Taylor 12013* (K, MO, NBG, PRE). Total number of specimens examined: 178.

20. **Lachnaea ericoides** *Meisn.* in DC., Prodromus systematis naturalis regni vegetabilis 14: 579 (1857); C.H.Wright: 24 (1915). Syntypes: Swellendam Dist., in mountains around Grootvadersbosch and Voormansbosch, altitude 3–5, October, *Ludwig s.n.* (not seen); *Zeyher 3776* (S, det. Meisner, lecto.!, here designated; PRE!, SAM!, Z!, isolecto.).

Gonophylla ericoides Eckl. & Zeyh. ex Meisn.: 579 (1857) nom. nud. in synonymy.

Erect, round to straggling, corymbosely or fastigiately branched shrub, up to 0.5 m tall, single-stemmed at base; reseeder. *Branches* ascending to inclined, slender, ridged below leaf bases, densely covered with long ascending or adpressed hairs admixed with crooked hairs later glabrescent, densely leafy, becoming naked with prominent leaf scars. *Leaves* alternate, subadpressed or ascending, usually falcate (apex curled inward), occasionally lower leaves of young plants straight, imbricate, sessile, epistomatic, narrowly-elliptic to obovate, 2–6(–8) × 0.8–1.5 mm, coriaceous, green, glabrous with tuft of hairs at apex which may become naked later; adaxially concave, smooth, dull, ± white-punctulate; abaxially convex, keeled, glossy, subpapillate; apex rounded or acute in straight leaves; base cuneate. *Inflorescence* a terminal, sessile, ebracteate, 2–8-flowered umbel with up to 4 open flowers at a time, on main flowering branches or also on lateral flowering branches restricted to area immediately below main inflorescence. *Flowers* subactinomorphic, cream. *Pedicel* 0.3–0.6 mm long, sericeous. *Hypanthium* 1.8–2.4 mm long, circumscissile $^1/_2$–$^2/_3$ from base; upper portion funnel-shaped, covered on outside with silky, straight, adpressed or crooked hairs, adpressed hirsute inside; basal portion oblong or narrowly ovoid to ovoid, glabrous outside and inside. *Sepals* erect-patent, subequal, narrowly elliptic to obovate, ovate to subrotund, 1.4–2.2 × 1.0–1.8 mm, apex rounded or obtuse, adaxially shortly tomentose to sparsely hairy, abaxially covered with crooked hairs admixed with long, silky, adpressed hairs. *Stamens* exserted; outer, antesepalous whorl arising at base of sepals, 0.8–1.2 mm long; inner, antepetalous whorl arising at rim of hypanthium, 0.5–0.9 mm long (inner stamens the shortest); anthers, spheroid, 0.3–0.6 mm long, abaxially without broad connective tissue. *Floral scales* exserted, arising at mouth of hypanthium immediately below antepetalous stamens, obovoid or subspheroid, 0.2–0.5 mm long, glabrous, translucent-white in fresh state. *Ovary* narrowly ellipsoid to obovoid, 0.7–0.8 mm long, glabrous. *Style* terete-obconical, 1.4–2.1 mm long, with ascending incurled hairs in the upper half. *Stigma* capitate and elongate-papillate with a few sparse hairs (Figure 46).

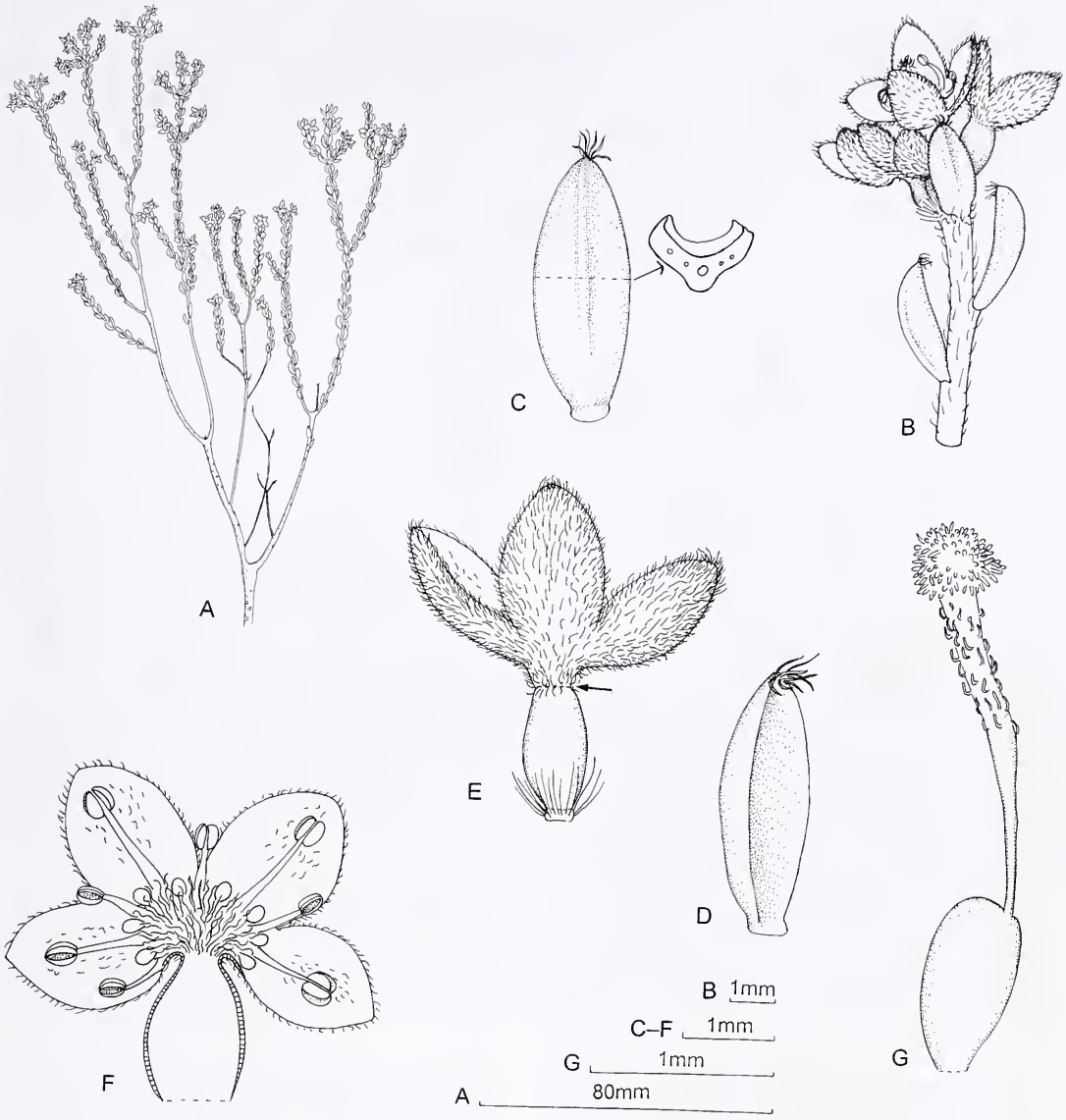

FIGURE 46.—*Lachnaea ericoides*, *Beyers 172* (NBG). A, portion of plant; B, flowering branch. C, D, leaves: C, abaxial view and c/s; D, lateral view. E, F, flower: E, circumscission zone arrowed; F, l/s with gynoecium removed. G, gynoecium. Scale bars: A, 80 mm; B–G, 1 mm.

Distribution and ecology

Lachnaea ericoides, a Langeberg endemic, occurs on the lower slopes from Clock Peaks in the Swellendam District to Garcia Forest Reserve in the Riversdale District at altitudes between 330 and 665 m (Figure 45). *Flowering time*: July, September to December.

Conservation status: Lower Risk Least Concern (LRlc). Frequent fires could result in this species rapidly moving into a threatened category.

Diagnostic characters and relationships

Lachnaea ericoides is closely related to *L. sociorum* but is distinguished by being a reseeder, the leaves being narrowly elliptic to obovate, adaxially keeled, with a rounded, tufted apex, the sepals being sericeous-tomentose adaxially and the capitate stigma having elongated papillae.

Vouchers: *Beyers 172* (K, MO, NBG, NY, PRE); *Esterhuysen 25034* (BOL, PRE); *McDonald 1621* (NBG, PRE), *1842* (NBG, PRE), *2027* (K, NBG, PRE); *Schlechter 1730* (BOL, S, Z). Total number of specimens examined: 62.

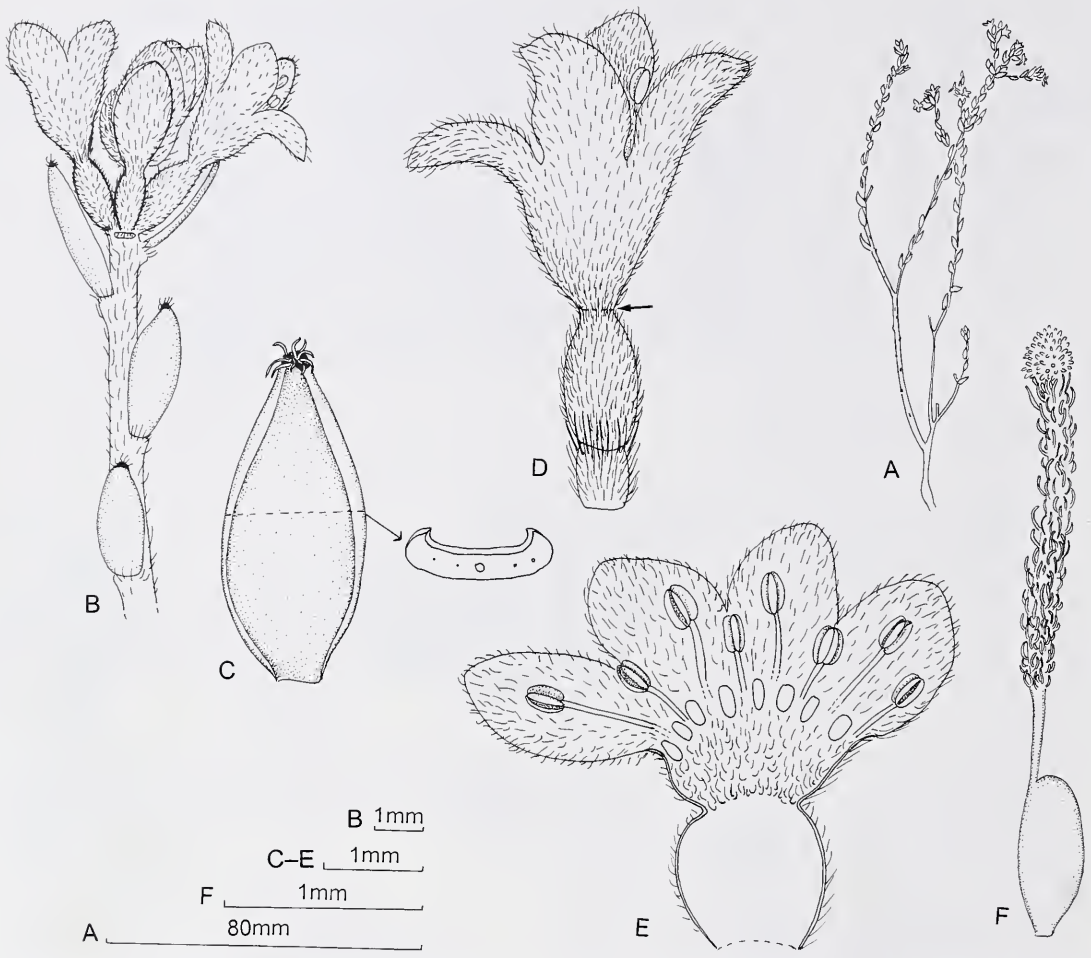

FIGURE 47.—*Lachnaea stokoei, Stokoe s.n. sub NBG103641* (NBG). A, portion of plant; B, flowering branch; C, leaf, adaxial view and c/s. D, E, flower: D, circumscission zone arrowed; E, l/s with gynoecium removed. F, gynoecium. Scale bars: A, 80 mm; B–F, 1 mm.

21. **Lachnaea stokoei** *Beyers*, sp. nov., *L. ericoidis* in facie similis foliis alternis anguste ellipticis ad ovatis marginibus involutis apicibus caespitosis inflorescentia umbellata ebracteata floribus tribus apertis simul, sed differt squamis inclusis, stigmate conico.

TYPE.—Western Cape, 3320 (Montagu): Swellendam Div., Langeberg Range, between Lemoenshoek and Noukrans Farm, Strawberry Hill, (–DD), 11-01-1957, *Stokoe s.n.* (*NBG103641*, holo.!; K!, *PRE49147*!, iso.).

Low shrublet, ?height. *Branches* ascending to inclined, slender, ridged below leaf bases, internodes $^1/_4$ to as long as leaves, densely covered with long stiff adpressed hairs admixed with crooked hairs, later glabrescent, densely leafy, becoming naked with prominent leaf scars. *Leaves* alternate, ascending, scattered, distal 4–5 leaves below inflorescence crowded, sessile, epistomatic, narrowly-elliptic to ovate, 2.5–4.0 × 1.0–1.5 mm, coriaceous, green, glabrous with tuft of hairs at apex which may become naked later; adaxially widely concave, smooth, dull, ± white-punctulate; abaxially ± flat, faintly nervate, glossy, margin involute; apex subacute; base cuneate. *Inflorescence* a terminal, sessile, ebracteate, 4–8-flowered umbel with up to 3 open flowers at a time, on main flowering branches. *Flowers* subactinomorphic, ?cream. *Pedicel* 0.4–0.8 mm long, sericeous. *Hypanthium* 3.2–4.2 mm long, circumscissile $^1/_2$–$^2/_5$ from base; upper portion obconical, sericeous outside, adpressed hairy inside; basal portion ellipsoid, sericeous outside, glabrous inside. *Sepals* ascending, subequal, elliptic to very widely ovate, 1.1–1.8 × 1.2–1.8 mm, apex rounded, sericeous on both sides. *Stamens* partly exserted; outer, antesepalous whorl exserted and inner, antepetalous whorl semi-exserted; antesepalous whorl arising at base of sepals to $^1/_4$ down upper portion of hypanthium; inner, antepetalous whorl arising $^1/_4$–$^1/_3$ down upper portion of hypanthium (inner stamens the shortest); outer filaments 0.7–1.0 mm long, inner 0.2–0.6 mm long; anthers, ellipsoid, 0.4–0.6 mm long, abaxially without broad connec-

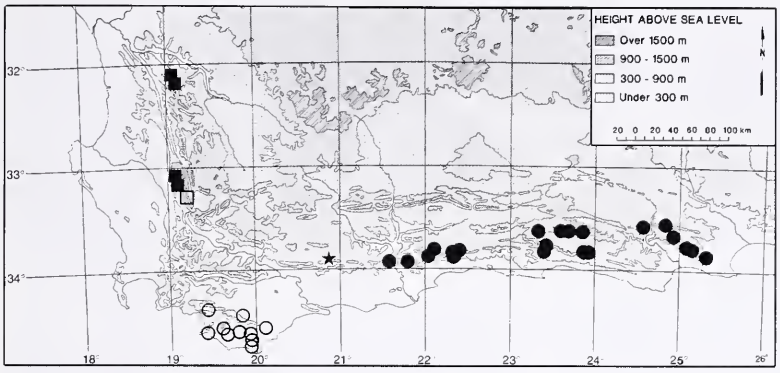

FIGURE 48.—Known distribution of *Lachnaea stokoei*, ★; *L. striata*, ■; *L. striata*, inexact locality, ❑; *L. aurea*, ○; and *L. burchellii*, ●.

tive tissue. *Floral scales* included, arising ± 1/3 down upper portion of hypanthium immediately below antepetalous stamens, semi-terete, elliptic in outline, abaxially attached to hypanthium, 0.3–0.4 mm long, glabrous. *Ovary* ellipsoid, 0.8–1.0 mm long, glabrous. *Style* terete-obconical, 2.2–3.0 mm long, with ascending incurled hairs throughout or only in upper three-quarters. *Stigma* conical and elongate-papillate (Figure 47).

Distribution and ecology

Lachnaea stokoei is a Langeberg endemic found in the Heidelberg District at Lemoenshoek [Grootberg] and Strawberry Hill, according to Stokoe's collections, dated December 1954 and January 1957. The localities given are very vague and no other more recent information is available about this species (Figure 48). *Flowering time*: December and January.

Conservation status: more than 40 years have elapsed since this species was last collected. The relevant portion of the Langeberg has been fairly well surveyed by McDonald (1993) and specific searches for this species have been unsuccessful. This species is therefore considered to be Extinct (Ex).

Diagnostic characters and relationships

Lachnaea stokoei resembles *L. ericoides* in general facies in that it has alternate, narrowly elliptic to ovate leaves with involute margins and tufts of hairs at the apices and the inflorescence which is an ebracteate umbel with up to three open flowers at a time, but the flower structure differs. The antesepalous stamen whorl is exserted, the antepetalous one semi-exserted, the floral scales arise abaxially ± a third of the way down the upper portion of the hypanthium and the stigma is conical and elongate-papillate.

Eponymy

This species is dedicated to T.P. Stokoe (1868–1959) who, as a member of the Mountain Club between 1913 and 1959, climbed extensively in the mountains of Western Cape where he collected many plant species new to science (Gunn & Codd 1981).

Vouchers: *Stokoe NBG103641, PRE49147, PRE49286, SAM69968, s.n.* (K). Total number of specimens examined: 5.

22. **Lachnaea striata** *(Poir.) Meisn.* in Linnaea 14: 415 (1840); Meisn. 577 (1857); C.H.Wright: 22 (1915). Type: *Passerina striata* in herb. Lam. (P-LA, –NBG, photocopy!).

Passerina striata Poir.: 44, t. 291, f. 2 (1804); non Spreng.: 240 (1825).

Gonophylla nervosa Eckl. & Zeyh. ex Meisn.: 577 (1857) nom. nud. in synonymy.

Lachnaea elegans Compton: 20 (1934a). Type: Cape Province; Ceres Div., exact locality unknown. Exhibited at Ceres Wild Flower Show, October 1932, *Compton 4157* (BOL, holo.!).

Erect, corymbosely branched shrublet up to 0.6 m tall, multistemmed at base; resprouter. *Branches* ascending, slender, slightly ridged below leaf bases, sericeous to sparsely sericeous, later glabrescent, densely leafy, becoming naked with prominent leaf scars. *Leaves* alternate, ascending, subimbricate to scattered, sessile, epistomatic, 4.8–10.0 × 1.5–4.5 mm, narrowly-elliptic to elliptic or ovate, coriaceous; adaxially flat with margin slightly incurved, glabrous, smooth, dull, ± white-punctulate; abaxially flat, venation conspicuous, prominently 1–5-ribbed, glabrous, glossy; apex acute; base cuneate to attenuate; margin crisped, ciliate, trichomes bulbous at base, base often tinged red; with age trichomes disappear, then margins papillate. *Inflorescence* a terminal, sessile, ebracteate, more than 12-flowered umbel, 8–20 mm diam., on main flowering branches. *Flowers* subactinomorphic, cream, purple or pale rose, pedicellate. *Pedicel* 0.4–0.9 mm long, sericeous. *Hypanthium* 2.6–4.2 mm long, circumscissile 1/2–2/3 from base; upper portion shortly funnel-shaped, sericeous to sparsely hairy outside, inside pubescent with stiff hairs at mouth; basal portion ellipsoid, glabrous outside and inside. *Sepals* patent, subequal, elliptic to ovate, 2.2–5.3 × 1.0–1.3 mm, apex rounded, adaxially sericeous or posterior and anterior ones sparsely hairy with apex sericeous, lateral ones glabrous, or all four glabrous and only sericeous at apex, abaxially sericeous. *Stamens* exserted; outer, antesepalous whorl arising at base of sepals; inner, antepetalous whorl arising at rim of hypanthium, shorter than outer whorl; outer filaments 1.0–1.6 mm long, inner 0.7–1.1

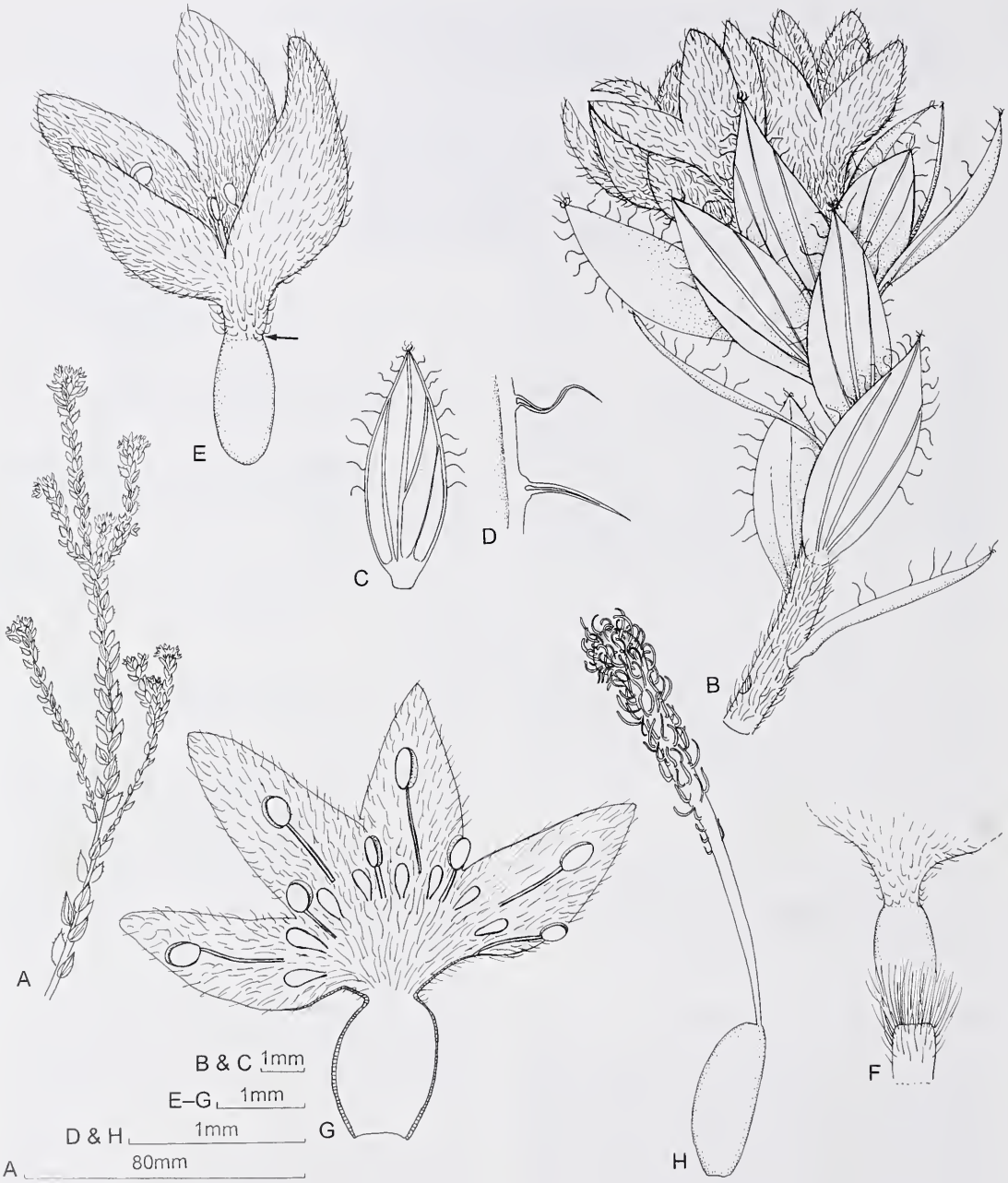

FIGURE 49.—*Lachnaea striata*, *Compton 6933* (NBG). A, portion of plant; B, flowering branch. C, D, leaf; C, abaxial view; D, margin with trichomes. E–G, flower: E, circumscission zone arrowed; F, basal portion with pedicel; G, l/s with gynoecium removed. H, gynoecium. Scale bars: A, 80 mm; B–H, 1 mm.

mm long; anthers widely ellipsoid to depressed spheroid, 0.5–0.7 mm long, abaxially without broad connective tissue. *Floral scales* exserted, arising at mouth of hypanthium immediately below antepetalous stamens, linear to clavate, 0.5–0.8 mm long, glabrous. *Ovary* ellipsoid, ovoid or obovoid, 1.0–2.2 mm long, glabrous. *Style* linear, 1.9–3.7 mm long, upper half covered with straight, adpressed or incurled hairs, lower half glabrous. *Stigma* brush-like (Figure 49).

Distribution and ecology

Lachnaea striata is known from the northern Cederberg around the Pakhuis and Heuningvlei areas

and south in the Groot Winterhoek, Witsenberg and Roodesand Mountains near Tulbagh, favouring seasonally damp areas at altitudes between 800 and 1 160 m (Figure 48). *Flowering time*: September to January.

Conservation status: Lower Risk Near Threatened (LRnt). The last known collection was made in 1971. It appears to be very rare and further searches are required to check the status of this species.

Diagnostic characters and relationships

Lachnaea striata is easily distinguished from the other species with alternate leaves and ebracteate inflorescences by its narrowly elliptic to ovate leaves with one to five prominent ribs abaxially and the crisped-ciliate margins.

Vouchers: *Bolus 9087* (BOL, NBG, PRE); *Ecklon & Zeyher 77.11* (GRA, SAM, S, Z); *Esterhuysen 21152* (BOL, PRE, S), *26861* (BOL, PRE); *Haynes 818* (NBG, PRE); *Stokoe BOL22326* (BOL, NBG, PRE). Total number of specimens examined: 32.

23. **Lachnaea aurea** *(Eckl. & Zeyh.) Meisn.* in DC.: 576 (1857); C.H.Wright: 21 (1915). Type: in mountains Klynriviersbergen [Klein River Mountains] near Hemel en Aarde, alt. 5, dist. Caledon, *Ecklon s.n.* [30 or 58.8] (NY [Meisner Herb.], holo.!; BOL!, GRA!, K!, NY [Torrey Herb.]!, PRE, SAM!, S!, Z!, iso.).

Erect, sparsely branched shrub up to 1 m tall, single- or few-stemmed at base; resprouter. *Branches* erect to flexuous, slender, ridged below leaf bases, adpressed-puberulent, leafy, becoming glabrous and naked with prominent leaf scars. *Leaves* alternate, adpressed or ascending, occasionally patent to reflexed, imbricate, sessile, epistomatic, narrowly elliptic or narrowly obovate, 7.5–18.0 × 0.8–4.0 mm, coriaceous, glabrous; adaxially flat or obtusely concave, smooth, dull, ± white-punctulate; abaxially obtusely convex, sometimes subkeeled just below apex, smooth, glossy; margin membranous, yellow in fresh state; apex acuminate; base cuneate; leaves below inflorescence broader with a wider membranous margin resembling involucral bracts, narrowly elliptic to elliptic or narrowly obovate to obovate 11.5–19.0 × 3.5–11.0 mm. *Inflorescence* a terminal, sessile, bracteate, more than 50-flowered, capitulum-like umbel with up to 30 open flowers at a time, 20–55 mm diam., on main flowering branches. *Involucral bracts* 6–8, narrowly elliptic to elliptic or obovate, 11.5–19.0 × 4.5–11.0 mm, innermost the widest, glabrous or abaxially sericeous along middle portion, ± flat or abaxially slightly keeled behind apex, middle portion coriaceous, 1- to 3-nervate, green; margin membranous, broad, yellow, sometimes tinged reddish purple at apex; apex mucronulate to mucronate or acuminate. *Flowers* zygomorphic, golden yellow, unscented, pedicellate. *Pedicel* 0.5–2.0 mm long, clothed with long, ascending, silky hairs. *Hypanthium* 3.8–7.8 mm long, circumscissile $^1/_2$–$^2/_3$ from base; upper portion narrowly funnel-shaped, clothed with long, ascending, silky hairs outside, inside adpressed hirsute; basal portion ellipsoid or ovoid, clothed with short, ascending, silky hairs outside and glabrous inside. *Sepals* patent, adaxially glabrous, abaxially sericeous, unequal, posterior one the smallest, ovate, acute to rounded, 2.6–4.5 × 1.6–3.0 mm, lateral ones narrowly elliptic, 7.5–14.0 × 2.0–3.5 mm, acute, anterior one usually the largest, narrowly elliptic, 9.3–15.5 × 3.0–4.5 mm, acute. *Stamens* exserted; outer, antesepalous whorl arising at base of sepals; inner, antepetalous whorl arising at rim of hypanthium; filaments 2.0–6.5 mm long; anthers ellipsoid, 0.8–1.5 mm long, abaxially without broad connective tissue. *Floral scales* exserted, arising at mouth of hypanthium immediately below antepetalous stamens, narrowly obovoid or ellipsoid, 0.8–1.4 mm long, apex occasionally irregularly lobed, glabrous, yellow in fresh state. *Ovary* ellipsoid or obovoid, 1.2–2.5 mm long, glabrous. *Style* terete-obconical, 4.0–6.5 mm long, adpressed hairy only in upper $^3/_4$. *Stigma* brush-like (Figure 50).

Distribution and ecology

Lachnaea aurea occurs from Hermanus to Bredasdorp and southwards to Agulhas on coastal flats and lower slopes, in acid sands and ferricrete at altitudes below 900 m (Figure 48). *Flowering time*: mostly in July to September, but occasionally in March, April and June.

Conservation status: Vulnerable (VU B1+2c). The habitat of this species has been restricted through the effects of agriculture and invasion by alien plants.

Diagnostic characters and relationships

Easily distinguished from the other umbellate species with alternate leaves by the showy, bracteate inflorescences with their strongly zygomorphic, golden yellow flowers, which at a glance appear asteraceous. *L. aurea* is a sister species of *L. striata*, both having leaves with marginal fibres not associated with the vascular bundles.

Vouchers: *Aggenbach s.n.* (K, MO, NBG, PRE, S, Z); *Beyers 135* (NBG); *Bolus 9186* (BOL, PRE, Z); *Compton 14777* (BOL, NBG, PRE); *Oliver 10550* (K, MO, NBG, NY, PRE, Z); *Schlechter 7610* (GRA, K, PRE, Z). Total number of specimens examined: 70.

24. **Lachnaea burchellii** *Meisn.* in Linnaea 14: 420 (1840); Meisn.: 577 (1857); C.H.Wright: 583 (1925). Type: Locality unknown, *Drège 7370* (P, holo.!; NY, capsule on *Ecklon 78*, iso.!).

Lachnaea phylicoides Lam. var. *oppositifolia* Meisn.: 420 (1840) nom. nud. in synonymy.

Gnidia tenuiflora Eckl. & Zeyh. ex Meisn.: 577 (1857) nom. nud. in synonymy.

Gonophylla nana Eckl. & Zeyh. ex Meisn.: 577 (1857) nom. nud. in synonymy.

Lachnaea burchellii var. *angustifolia* Meisn.: 577 (1857). Syntypes: locality unknown, *Drège 7370*, (P!, NY, capsule on *Ecklon 78*!); in mountains, Dist. George, alt. 5, *Ecklon & Zeyher s. n.* (not seen).

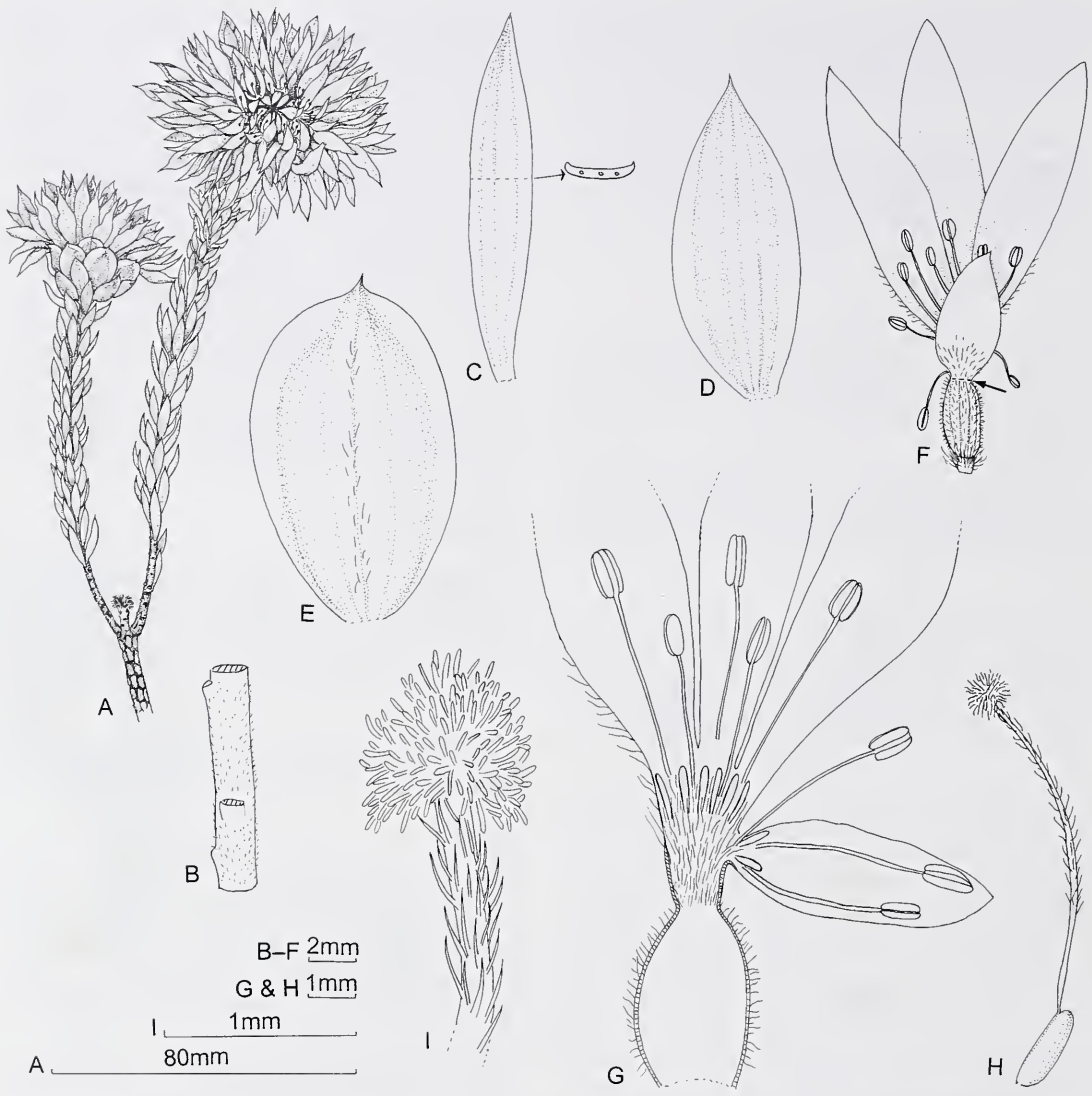

FIGURE 50.—*Lachnaea aurea*, *Oliver 10550* (NBG). A, portion of plant; B, branch with leaves removed; C, leaf, abaxial view and c/s. D, E, involucral bracts: D, from subdistal pair; E, from distal pair. F, G, flower: F, circumscission zone arrowed; G, l/s with gynoecium removed. H, gynoecium; I, stigma and upper portion of style. Scale bars: A, 80 mm; B–F, 2 mm; G–I, 1 mm.

Lachnaea burchellii var. *latifolia* Meisn.: 577 (1857); C.H.Wright: 583 (1925). Syntypes: in mountains, at Vanstadesrivier [Van Stadens River], alt. 2–4, Dist. Uitenhage, *Ecklon 78* (NY [Meisner Herb.]!, lecto., here designated; GRA!, NY [Torrey Herb]!, PRE!, S!, Z!); *Zeyher 3757* (K!, PRE!, SAM!, Z!).

Erect to decumbent, sparsely branched shrub up to 0.3 m tall, single-stemmed at base; reseeder. *Branches* erect to straggling, slender, ridged below leaf bases, internodes $^1/_2$–2 × as long as leaves, sparsely adpressed hairy or glabrous, leafy, becoming naked with prominent leaf scars. *Leaves* decussate or occasionally subopposite, ascending to inclined, distal pair below inflorescence patent, imbricate to scattered, sessile, epistomatic, lanceolate to narrowly elliptic, 6–13 × 1–3 mm, coriaceous, glabrous, ± flat; adaxially smooth, dull, ± white-punctulate; abaxially 1–3-ribbed, glossy; apex acuminate; base cuneate; leaves on reduced lateral flowering branches bract-like, elliptic, obovate to widely obovate or suborbicular, 1.3–4.9 × 1.1–4.5 mm, coriaceous, green, often with reddish tinge; adaxially concave, smooth, dull; abaxially convex, glossy, obtuse or mucronate, glabrous or abaxially sparsely hairy; margin ciliate. *Inflorescence* a terminal, sessile, ebracteate, 4–10-flowered umbel on main and short lateral flowering branches, those on the latter appearing bracteate. *Flowers* subactinomorphic, cream or pale pink. *Pedicel* 0.3–1.1 mm long, adpressed hirsute. *Hypanthium* 2.3–4.6 mm long, circumscissile $^1/_2$–$^2/_3$ from base; upper portion funnel-shaped, sericeous outside, adpressed hir-

sute inside; basal portion ellipsoid or ovoid, clothed with obtuse hairs outside, glabrous inside. *Sepals* patent, subequal, posterior sepal smallest, anterior one largest, elliptic or ovate, 2.0–4.6 × 1.1–3.2 mm, apex rounded or obtuse, adaxially sparsely sericeous or glabrous, abaxially sericeous. *Stamens* exserted; outer, antesepalous whorl arising at base of sepals; inner, antepetalous whorl arising at rim of hypanthium; filaments 0.7–1.4 mm long; anthers ellipsoid to suborbicular, 0.5–0.7 mm long, abaxially without broad connective tissue. *Floral scales* exserted, arising at mouth of hypanthium immediately below antepetalous stamens, capitate, 0.4–0.5 mm long, lower half with declinate trichomes, upper half glabrous, white in fresh state. *Ovary* ellipsoid, 0.8–1.4 mm long, glabrous. *Style* terete-obconical, 2.1–3.7 mm long, clothed with stiff ascending hairs in upper half. *Stigma* brush-like (Figure 51).

Distribution and ecology

Lachnaea burchellii occurs on mountain slopes from Albertinia in Western Cape eastwards to Port Elizabeth in Eastern Cape, at altitudes between 330 and 1 660 m (Figure 48). *Flowering time*: June to March.

Conservation status: Lower Risk Least Concern (LRlc).

Diagnostic characters

Lachnaea burchellii is distinguished from *L. glomerata* by being a reseeder, and in having the outside of the upper portion of the hypanthium and the sepals sericeous, with clavate trichomes on the outside of the basal portion of the hypanthium and a brush-like stigma.

Vouchers: *Esterhuysen 10778* (BOL, NBG, PRE); *Oliver 9241* (K, MO, NBG, PRE), *9251* (K, NBG, PRE), *9941* (K, MO, NBG, PRE); *Spreeth 155* (K, MO, NBG, PRE); *Thompson 1842* (NBG, PRE). Total number of specimens examined: 118.

25. **Lachnaea glomerata** *Fourc.* in Transactions of the Royal Society of South Africa 21: 101 (1934). Type: Div. Humansdorp: Klein Hoek, 1000 ft, Sept. 1909, *Fourcade 445* (BOL, holo.!; NBG!, iso.).

Erect, moderately branched shrub up to 0.45 m tall, multi-stemmed at base; resprouter. *Branches* erect, slender, ridged below leaf bases, internodes $^1/_2$–$^2/_3$ as long as leaves, sparsely adpressed hairy or glabrous, leafy, becoming naked with prominent leaf scars. *Leaves* decussate, ascending to patent, scattered, sessile, epistomatic, linear-elliptic to elliptic or obovate, 4.0–10.5 × 1–2 mm, coriaceous, glabrous; adaxially concave, smooth, dull, ± white-punctulate; abaxially convex, smooth or subkeeled, glossy; apex mucronate or acuminate; base cuneate; distal 2 or 3 or occasionally 4 or 5 leaf pairs immediately below inflorescence bract-like, elliptic, ovate, obovate or suborbicular, 1.3–3.0 × 1.3–2.4 mm, coriaceous; adaxially concave; abaxially convex, keeled to subkeeled, mucronate; margin ciliate. *Inflorescence* a terminal, sessile, ebracteate, 6–8-flowered umbel, 5–10 mm diam., on main and also on short lateral flowering branches below main inflorescence thus appearing racemose-like. *Flowers* subactinomorphic, cream or pale pink, sweetly skunk-scented. *Pedicel* 0.3–0.5 mm long, adpressed hirsute. *Hypanthium* 1.5–1.9 mm long, circumscissile ± $^1/_2$ way; upper portion funnel-shaped, tomentose outside, adpressed hirsute inside; basal portion ellipsoid, tomentose outside, glabrous inside. *Sepals* patent, subequal, elliptic to widely elliptic, 1.4–3.0 × 1–2 mm, apex rounded or obtuse, adaxially sparsely tomentose to glabrescent, abaxially tomentose. *Stamens* exserted; outer, antesepalous whorl arising at rim of hypanthium; inner, antepetalous whorl arising at mouth of hypanthium; filaments 0.4–1.0 mm long; anthers ellipsoid to suborbicular, 0.2–0.4 mm long, abaxially without broad connective tissue. *Floral scales* exserted, arising at mouth of hypanthium immediately below antepetalous stamens, clavate, 0.3–0.5 mm long, glabrous, yellow in fresh state. *Ovary* ellipsoid, 0.8–0.9 mm long, glabrous. *Style* terete-obconical, 1.3–1.9 mm long, with straight, adpressed or incurled hairs in upper half. *Stigma* capitate, elongate-papillate (Figure 52).

Distribution and ecology

Lachnaea glomerata has been recorded from mountains in the Little Karoo, from Antoniesberg in the Willowmore District and from Kleinhoek in the Humansdorp District growing in stony soil on Table Mountain Sandstone at altitudes between 330 and 1 130 m (Figure 53). *Flowering time*: August to October.

Conservation status: Lower Risk Least Concern (LRlc).

Diagnostic characters

Lachnaea glomerata is distinguished from *L. burchellii* by being a resprouter, and in having the outside of the hypanthium and sepals tomentose, acicular trichomes on the outside of the upper and lower portions of the hypanthium and a capitate, elongate-papillate stigma.

Vouchers: *Beyers 192* (BOL, K, MO, NBG, NY, PRE, S, WU, Z); *Esterhuysen 24977* (BOL); *Euston-Brown 117* (BOL, NBG), *485* (GRA, NBG), *551* (K, NBG, PRE); *Vlok 2378* (K, NBG, PRE). Total number of specimens examined: 33.

26. **Lachnaea laniflora** *(C.H.Wright) Bond* in Journal of South African Botany 48: 527 (1982). Type: Clanwilliam Div., Cederberg Range, Sneeukop, 4500 ft, *Bodkin in Herb. Bolus 9086* (BOL, holo.!; NBG!, iso.).

Passerina laniflora C.H.Wright: 11 (1915).

Rounded, compact, much-branched shrub up to 1 m tall and up to 2 m diam., single-stemmed at base, branching close to ground; reseeder. *Branches* ascending to patent, subrigid to flexuose, terete, internodes $^1/_5$–$^1/_2$ length of leaves, at first tomentose, later glabrescent, leafy, becom-

FIGURE 51.—*Lachnaea burchellii*, *Oliver 9251* (NBG). A, portion of plant; B, flowering branch; C, leaf, abaxial view and c/s. D, E, flower: D, circumscission zone arrowed; E, l/s with gynoecium removed. F, scale; G, gynoecium. Scale bars: A, 80 mm; B, 2 mm; C–G, 1 mm.

ing naked with prominent leaf scars. *Leaves* decussate, usually strictly four-ranked, ascending, slightly incurved, imbricate, sessile, epistomatic, coriaceous, narrowly ovate to narrowly elliptic, 2.5–7.0 × 0.9–1.3 mm, glabrous; adaxially obtusely concave or concave, enervate, white-punctulate, dull; abaxially convex, keeled, usually more so

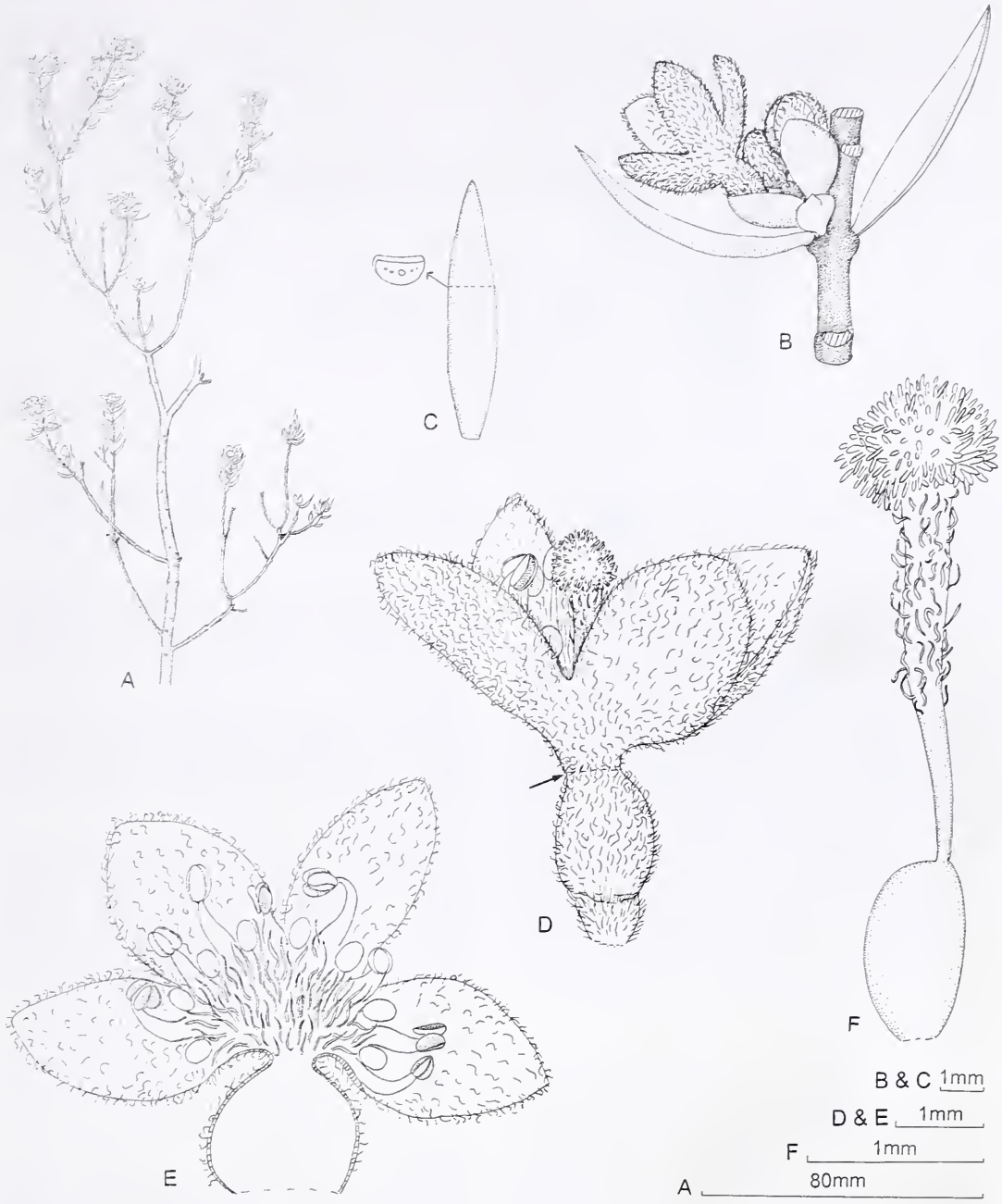

FIGURE 52.—*Lachnaea glomerata*, *Beyers 192* (NBG). A, portion of plant; B, frowering branch; C, leaf, abaxial view and c/s. D, E, flower: D, circumscission zone arrowed; E, l/s with gynoecium removed. F, gynoecium. Scale bars: A, 80 mm; B–F, 1 mm.

towards apex, glossy; apex rounded or occasionally mucronulate; base rounded or obtuse; 2 distal leaf pairs subtending inflorescence bract-like, elliptic to widely elliptic or obovate, 2.9–5.1 × 2.1–3.0 mm, coriaceous, glabrous, green or green tinged reddish brown; adaxially concave; abaxially convex, keeled towards apex; margin glabrous or occasionally ciliolate; apex subacute; base cuneate or rounded. *Inflorescence* a terminal, sessile, pseudobracteate, ± 15-flowered, capitulum-like umbel with up to 14 open flowers at a time, 5–15 mm diam., on main flowering branches; umbel appears to be enclosed at base by 2 pairs of involucral bracts but vegetative shoots were observed to develop in axils of bract-like leaves. *Flowers* ± actinomorphic, pink, white, white tinged violet-blue, white turning

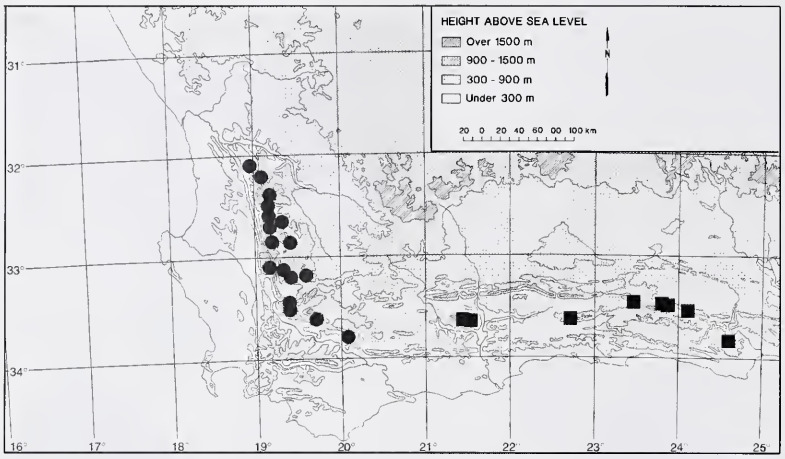

FIGURE 53.—Known distribution of *Lachnaea glomerata*, ■; and *L. laniflora*, ●.

pink with age or occasionally dark red to reddish brown, pedicellate. *Pedicel* 0.2–0.7 mm long, not noticeably elongating in fruit, sericeous. *Hypanthium* 2.3–4.0 mm long, circumscissile ± 1/3–1/2 from base, circumscission zone not clearly defined; upper portion funnel-shaped, sericeous or sericeous-tomentose outside, sericeous inside; basal portion ellipsoid, outside puberulent to sericeous in upper half, rest glabrous, inside glabrous. *Sepals* patent, ± equal, elliptic to widely elliptc, 1.6–4.2 × 1.0–2.3 mm, adaxially sericeous to sparsely adpressed hairy, occasionally glabrous, abaxially sericeous, apex rounded. *Stamens* exserted; outer, antesepalous whorl arising at base of sepals; inner, antepetalous whorl arising at rim of hypanthium, shorter than outer whorl; outer filaments 0.9–1.7 mm long, inner 0.6–1.3 mm long; anthers widely ellipsoid to spheroid, 0.2–0.5 mm long, abaxially without broad connective tissue. *Floral scales* exserted, arising at mouth of hypanthium immediately below antepetalous stamens, narrowly ellipsoid or narrowly obovoid, 0.4–1.0 mm long, glabrous, yellow or white in fresh state. *Ovary* ellipsoid, 0.7–1.0 mm long, glabrous. *Style* terete-obconical, 2.1–3.4 mm long, sericeous in upper half. *Stigma* brush-like (Figure 54).

Distribution and ecology

Lachnaea laniflora is known from Pilaarsberg in the northern Cederberg southwards along the Skurweberge and the Groot Winterhoek Mountains to Brandwag Peak northwest of Worcester and eastwards to the western end of the Langeberg near Montagu, usually growing amongst rocks or in rock crevices, at altitudes between 1 000 and 2 200 m (Figure 53). *Flowering time*: July to March.

Conservation status: Lower Risk Least Concern (LRlc).

Diagnostic characters and relationships

Lachnaea laniflora is easily distinguished by the imbricate, usually four-ranked leaves which are slightly incurved and keeled abaxially, the pseudobracteate capitulum-like umbels with ± actinomorphic flowers, and terete pedicels which hardly elongate in the fruiting stage. Its taxonomic affinities are unclear.

Vouchers: *Brown 500* (NBG, PRE); *Compton 16706* (BOL, NBG, S); *Forsyth 51* (NBG, PRE); *Oliver 9045* (NBG, PRE), *10679* (BOL, K, MO, NBG, PRE); *Schlechter 10220* (BOL, GRA). Total number of specimens examined: 77.

27. **Lachnaea elsieae** *Beyers*, sp. nov., *L. penicillatae* structura floris affinis, sed umbella pseudobracteata floribus usque ad quatuor simul apertis, styloque glabro differt.

TYPE.—Western Cape, 3219 (Wuppertal): Cold Bokkeveld, Tafelberg at Boplaas, S–SE of Tafelberg, slopes, 1 350 m, (–CD), 4-04-1998, *Hanekom 3013* (NBG, holo.!; BOL!, K!, MO!, NY!, P!, PRE!, S!, Z!, iso.).

Compact, rounded or diffuse spreading, much-branched shrub up to 0.6 m tall, single-stemmed at base branching near ground, or multistemmed at base; reseeder or resprouter. *Branches* ascending to patent, slender, terete, internodes 1/2 to as long as leaves, felted, tomentose or villous-tomentose, leafy, later glabrescent and naked without prominent leaf scars. *Leaves* decussate, adpressed or subadpressed, scattered, those below inflorescence crowded, sessile, epistomatic, narrowly ovate to ovate or narrowly elliptic to elliptic, 1.0–4.5 × 0.4–1.1 mm, coriaceous; adaxially concave, enervate, dull; abaxially convex, subkeeled or keeled, glossy, glabrous, margin of distal leaves below inflorescence sparsely villous-ciliate; apex rounded, villous-tufted; base rounded; distal 2 leaf pairs subverticillate, bract-like, partially enclosing inflorescence, coriaceous, green or occasionally tinged maroon, glabrous; adaxially concave; abaxially convex, subkeeled or keeled in upper half; distal pair elliptic or obovate to widely obovate, 1.6–3.3 × 0.9–2.0 mm; margin membranous or brown scarious, ciliate; apex subacute to obtuse or emarginate; subdistal pair narrowly elliptic to elliptic, ovate or obovate, 1.8–4.0 × 0.9–1.5, margin membranous or brown scarious, villous-ciliate; apex acute to rounded. *Inflorescence* a terminal, sessile, 3–13-flowered, pseudobracteate umbel with 1–4 open flowers at a time, up to 2 mm diam., on main flowering branches or also on short lateral flowering branches just

FIGURE 54.—*Lachnaea laniflora*, *Oliver 10679* (NBG). A, portion of plant; B, flowering branch; C, leaf, abaxial view and c/s. D, E, bract-like leaves subtending inflorescence: D, from subdistal pair; E, from distal pair. F–H, flower: F, view from above; G, side view and circumscission zone arrowed; H, l/s with gynoecium removed. I, gynoecium; J, stigma and upper portion of style. Scale bars: A, 80 mm; B–J, 1 mm.

below main inflorescence or for some distance down main flowering branch, thus either forming a cluster of inflorescences at apex of main flowering branches or appearing racemose-like on main flowering branches. *Flowers* subactinomorphic, cream, pale pink or cream turning pink or pale, dull red with age, pedicellate. *Pedicel* 0.3–1.4 mm long, covered with long silky, ascending hairs becoming villous with age, elongating in fruiting stage. *Hypanthium* 1.2–2.3 mm long, circumscissile ± $^1/_2$ way; upper portion shortly funnel-shaped, sericeous outside, adpressed hirsute inside; basal portion ellipsoid or oblong, outside puberulent in upper $^1/_2$ to upper $^1/_3$, glabrous below, inside glabrous. *Sepals* erect-patent to patent, subequal, ovate to widely

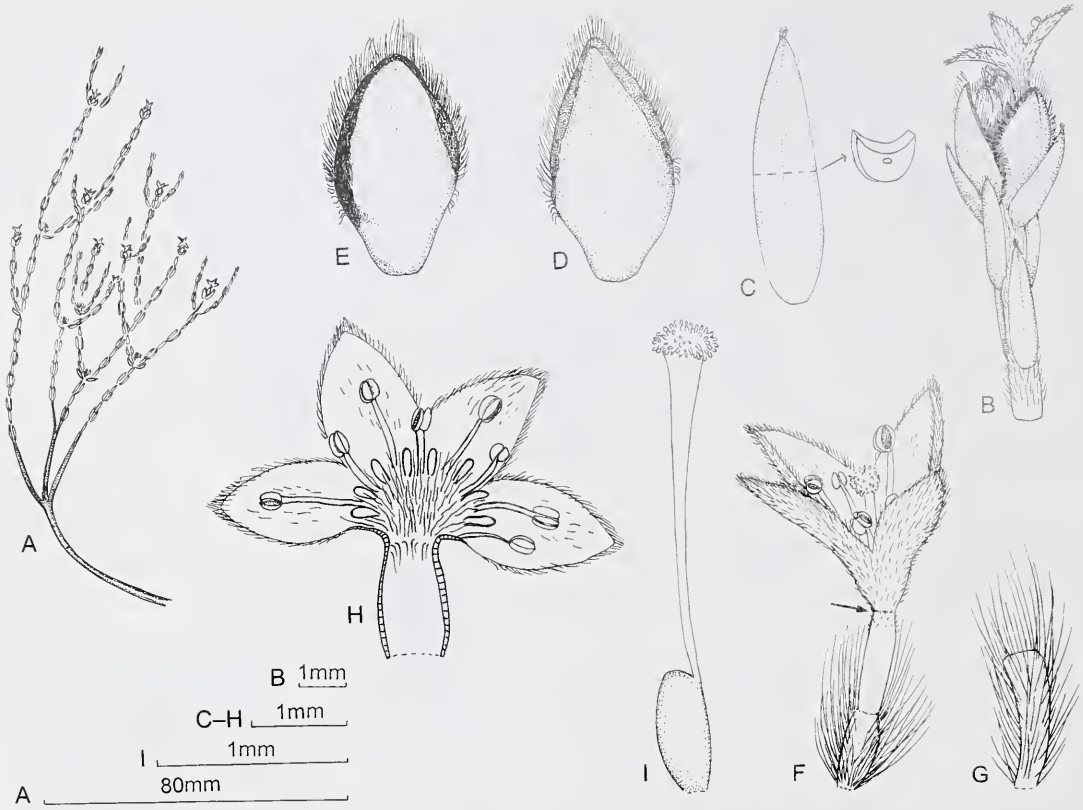

FIGURE 55.—*Lachnaea elsieae*. A, portion of plant; B, flowering branch; C, c/s leaf. D, E, bract-like leaves subtending inflorescence: D, from subdistal pair; E, from distal pair. F, H, flower: F, circumscission zone arrowed; H, l/s with gynoecium removed. G, elongated pedicel in fruiting stage; I, gynoecium. A, *Boucher 5077* (NBG); B–I, *Hanekom 3013* (NBG). Scale bars: A, 80 mm; B–I, 1 mm.

ovate or elliptic to widely ovate, 1.0–1.9 × 0.5–1.4 mm, apex subacute or rounded, adaxially glabrous or sparsely adpressed hairy in upper half, abaxially sericeous. *Stamens* exserted; outer, antesepalous whorl arising at base of sepals; inner, antepetalous whorl arising at rim of hypanthium; outer filaments 0.4–1.0 mm long, inner 0.3–0.8 mm long; anthers ellipsoid to spheroid, 0.2–0.4 mm long, abaxially without broad connective tissue. *Floral scales* exserted, arising in mouth of hypanthium immediately below antepetalous stamens, obovoid, 0.2–0.6 mm long, glabrous, translucent white or pale yellow in fresh state. *Ovary* narrowly ellipsoid to obovoid, 0.6–1.1 mm long, glabrous. *Style* terete-obconical, 1.1–2.2 mm long, glabrous. *Stigma* capitate, elongate-papillate (Figure 55).

Distribution and ecology

Lachnaea elsieae ranges from Sneeukop in the Cederberg southwards to the northeastern Cold Bokkeveld and eastwards along the mountains of the Little Karoo as far east as Seweweekspoort in the Ladismith District. It seems to occur on shale bands and adjacent sandstone-derived soil at altitudes between 1 250 and 2 300 m (Figure 56).

Heavily grazed individuals have a dense, compact and rounded habit, appearing quite different from the ungrazed ones which have a loose, slender, almost decumbent habit. *Flowering time*: throughout the year.

Conservation status: Lower Risk Least Concern (LRlc).

Diagnostic characters and relationships

Lachnaea elsieae superficially resembles *L. penicillata*, a distantly related species, but differs in having a pseudobracteate umbel, with up to four open flowers at a time, and a glabrous style.

Eponymy

This species is dedicated to Ms Elsie Esterhuysen, one of southern Africa's most eminent plant collectors of the 20th century. Her collections, especially those of the montane species of *Lachnaea*, have been invaluable in the classification of the group.

Vouchers: *Forsyth 532* (K, NBG, PRE); *Hanekom 3000* (K, MO, NBG, PRE, S); *Moffett & Steensma 3863* (NBG, PRE); *Oliver 9689* (BOL, K, NBG, NY, P, PRE,), *11489* (K, NBG, PRE); *Schlechter 10072* (BOL, K, NBG, PRE, S, Z). Total number of specimens examined: 103.

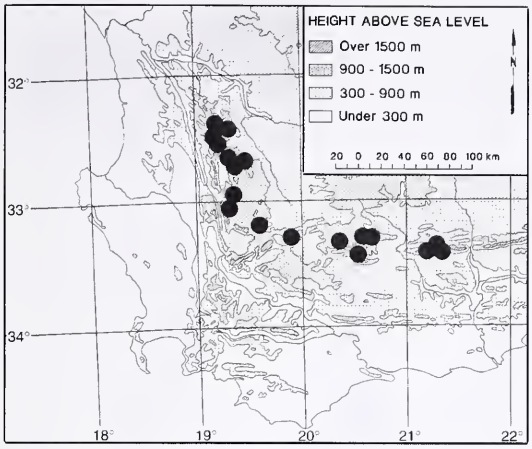

FIGURE 56.—Known distribution of *Lachnaea elsieae*.

28. **Lachnaea villosa** *Beyers*, sp. nov., primo adspectu *L. funicaulis* similis, sed differt inflorescentia pseudobracteata (non bracteata), parte superiore hypanthii sepalorumque extra villoso-tomentosa (non tomentoso-sericea), squamis exsertis et in ore hypanthii exorientibus (non inclusis).

TYPE.—Western Cape, 3319 (Worcester): Ceres Dist., Schoonvlei, 480 m, (–AD), 24-01-1989, *Beyers 125* (NBG, holo.!; BOL!, K!, MO!, NY!, P!, PRE!, iso.).

Compact or sparsely branched, erect to sprawling shrub up to 0.5 m tall, single-stemmed at base or branching at base, appearing multistemmed; reseeder. *Branches* ascending to inclined, slender, terete, internodes $^2/_3$ to $1^1/_2$ as long as leaves, felted, leafy, later glabrescent and naked without prominent leaf scars. *Leaves* decussate, adpressed, scattered, those below inflorescence crowded, sessile, epistomatic, lanceolate or narrowly elliptic, 2.8–5.0 × 0.6–1.2 mm, coriaceous, glabrous with lanate-ciliate margin, terminal hairs simulating a mucro, later margins glabrescent; adaxially concave, smooth, dull; abaxially convex, keeled or subkeeled, glossy; apex rounded or acute; base rounded; distal 2 leaf pairs subverticillate, bract-like, broader and thinner than other leaves, margin brown, lanate-ciliate; distal pair obovate or widely elliptic, 2.3–3.1 × 1.6–2.2 mm, apex rounded or obtuse; subdistal pair elliptic or obovate, 2.7–3.2 × 1.1–1.4 mm, apex rounded. *Inflorescence* a terminal, sessile, 12–20-flowered, capitulum-like, pseudobracteate umbel with 1–3, occasionally 5 open flowers at a time, 3–6 mm diam., on main and sometimes on short lateral flowering branches just below main inflorescence forming a cluster of inflorescences at apex; umbel appears to be enclosed at base by 2 pairs of involucral bracts but vegetative shoots were observed to develop in axils of distal bract-like leaf pair. *Flowers* ± actinomorphic, cream, sweetly scented, pedicellate. *Pedicel* 0.7–2.8 mm long, covered with ascending, crisped hairs in fresh state, villous in dry state, elongating in fruiting stage. *Hypanthium* 2–3 mm long, circumscissile $^1/_3$–$^2/_3$ from base; upper portion funnel-shaped, villous-tomentose outside, villous-hirsute inside; basal portion ellipsoid, outside towards circumscission zone puberulent, below glabrous, inside glabrous. *Sepals* erect-patent, subequal, elliptic to widely elliptic or ovate to widely ovate, 1.2–1.7 × 0.8–1.1 mm, apex rounded or obtuse, adaxially glabrous or distal $^1/_3$ villous-tomentose, abaxially villous-tomentose. *Stamens* exserted; outer, antesepalous whorl arising at base of sepals usually close to rim of hypanthium; inner, antepetalous whorl arising at rim of hypanthium; outer filaments 0.5–0.9 mm long, inner 0.4–0.6 mm long; anthers spheroid, 0.2–0.3 mm long, abaxially without broad connective tissue. *Floral scales* exserted, arising in mouth of hypanthium just below antepetalous stamens, capitate, 0.2–0.4 mm long, glabrous, yellow in fresh state. *Ovary* narrowly obovoid, ovoid or ellipsoid, 0.4–1.0 mm long, glabrous. *Style* terete-obconical, 1.0–2.3 mm long, glabrous. *Stigma* capitate, papillate (Figure 57).

Distribution and ecology

Lachnaea villosa has been recorded from the northern Bokkeveld in the Citrusdal District southwards to Schoonvlei north of Ceres in sandy or stony soil on the lower slopes and flats at altitudes between 480 and 1 500 m (Figure 58). *Flowering time*: throughout the year.

Conservation status: Lower Risk Least Concern (LRlc).

Diagnostic characters and relationships

Lachnaea villosa superficially resembles *L. funicaulis* but differs in its inflorescence and floral structure. In *L. villosa* the inflorescence is pseudobracteate (not bracteate), the upper portion of the hypanthium and sepals are villous-tomentose on the outside (not tomentose-sericeous) and the floral scales are exserted (not enclosed), and arise in the mouth of the hypanthium, (not midway to four-fifths down the upper portion of the hypanthium). It is allied to *L. elsieae* but can be distinguished from it by being a reseeder, having lanate-ciliate leaves, the upper portion of the hypanthium and sepals being villous-tomentose and by the capitate floral scales.

Etymology

The specific epithet, *villosa*, refers to the long, soft, curly trichomes in the indumentum on the sepals.

Vouchers: *Boucher 1973* (NBG, PRE, S); *Dahlgren & Peterson 270* (K, NBG); *Hanekom 2937* (BOL, K, MO, NBG, PRE), *3005* (K, MO, NBG, P, PRE, S, WU, Z); *Oliver 9808* (K, NBG, PRE), *10400* (K, MO, NBG, PRE); *Schlechter 10066* (BOL, PRE, S, Z). Total number of specimens examined: 123.

29. **Lachnaea marlothii** *Schltr.* in Journal of Botany, British and Foreign 34: 503 (1896). Syntypes: in southwestern region: Matroosberg, in grassy mountain slopes, alt. 6000–6500 ft, Dec. 1895, *Marloth 2218* (NBG, lecto.!, here designated; BOL!, PRE!, isolecto.); *Marloth 2276* (PRE!).

Note: Schlechter did not annotate any of the above sheets, but he most probably saw the material during his two visits to South Africa

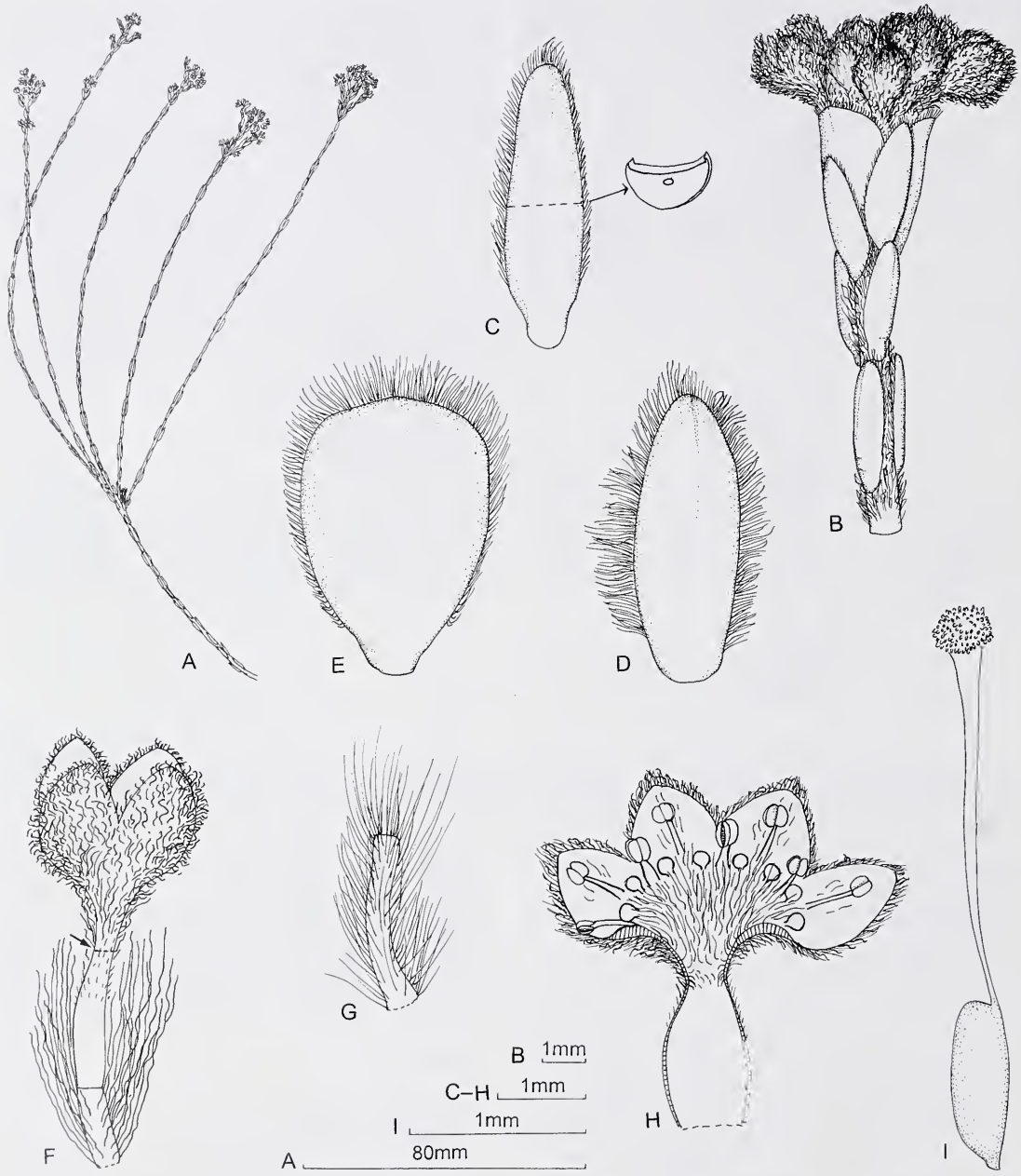

FIGURE 57.—*Lachnaea villosa*, *Beyers 125* (NBG). A, portion of plant; B, flowering branch; C, leaf, abaxial view and c/s. D, E, bract-like leaves subtending inflorescence: D, from subdistal pair; E, from distal pair. F, H, flower: F, circumscission zone arrowed; H, l/s with gynoecium removed. G, elongated pedicel in fruiting stage; I, gynoecium. Scale bars: A, 80 mm; B–I, 1 mm.

between 1891 and 1898 (Gunn & Codd 1981). *Marloth 2218* consisting of three sheets, one in each of the main South African herbaria, is chosen as the lectotype.

Slender, spreading or cushioned, moderately branched shrub up to 0.3 m tall, appearing multistemmed at base; regeneration unknown. *Branches* ascending to patent, slender, terete, internodes $^1/_4$–$^3/_4$ as long as leaves, felted or thinly tomentose, leafy, later becoming glabrous and naked without prominent leaf scars. *Leaves* decussate, adpressed or ascending, scattered, those below inflorescence crowded, sessile, epistomatic, narrowly elliptic, 2.5–4.2 × 0.6–1.0 mm, coriaceous; adaxially concave, enervate, dull; abaxially convex, subkeeled in upper half, glossy, glabrous; apex rounded, at first villous-tufted, later naked; base rounded; distal 2 leaf pairs subverticillate, partially enclosing inflorescence, broader than other leaves, bract-like, coriaceous, green or green

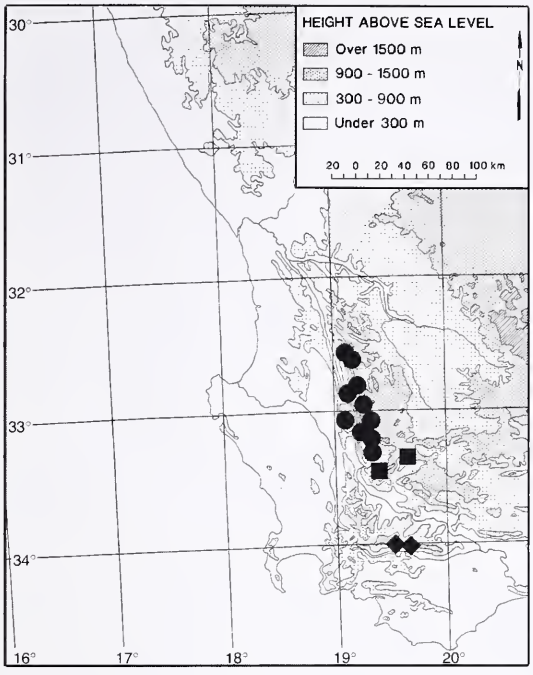

FIGURE 58.—Known distribution of *Lachnaea villosa*, ●; *L. marlothii*, ■; and *L. greytonensis*, ◆.

with maroon tinge, glabrous, adaxially concave, abaxially convex, keeled in upper half; elliptic or obovate, 2.9–4.1 × 1.2–2.7 mm; margin villous-cilliate; apex acute to obtuse. *Inflorescence* a terminal, sessile, 5–8-flowered, pseudobracteate umbel with 2–4 open flowers at a time, 5–10 mm diam., on main flowering branches. *Flowers* subactinomorphic, cream or cream with pink tinge, pedicellate. *Pedicel* 0.5–0.7 mm long, villous, elongating in fruiting stage. *Hypanthium* 1.8–3.2 mm long, circumscissile $^1/_2$–$^2/_3$ from base; upper portion funnel-shaped, sericeous-pilose outside, adpressed hirsute inside; basal portion ellipsoid, glabrous on both sides. *Sepals* erect-patent, subequal, elliptic, 2.0–2.4 × 0.8–1.3 mm, apex rounded or obtuse, adaxially glabrous or adpressed hairy in upper quarter, abaxially sericeous-pilose. *Stamens* exserted; outer, antesepalous whorl arising a $^1/_3$-way up on sepals; inner, antepetalous whorl arising on rim of hypanthium; outer filaments 0.7–1.0 mm long, inner 0.6–1.0 mm long; anthers ellipsoid to spheroid, 0.3–0.5 mm long, abaxially without broad connective tissue. *Floral scales* exserted, arising immediately below antepetalous stamens in mouth of hypanthium, capitate or obovoid, 0.2–0.4 mm long, glabrous, yellow in fresh state. *Ovary* ellipsoid, 0.8–1.0 mm long, glabrous. *Style* terete-obconical, 1.8–2.5 mm long, glabrous. *Stigma* capitate, elongate-papillate (Figure 59).

Distribution and ecology

Lachnaea marlothii is confined to the Hex River Mountains at altitudes between 1 800 and 2 330 m (Figure 58). *Flowering time*: August and December.

I have not been able to study this species in the live state and unfortunately very little information could be obtained from the herbarium labels.

Conservation status: this species has a restricted, localized distribution and its mode of regeneration is not known. The status of Vulnerable (VU D2) seems appropriate.

Diagnostic characters and relationships

Lachnaea marlothii can easily be confused with *L. elsieae*, a distant relative. Both belong to the group of species with pedicels that elongate in the fruiting stage. *L. marlothii*, however, is distinguished from *L. elsieae* by the upper portion of the hypanthium and the sepals being villous-pilose on the outside, the capitate or obovate floral scales and the antesepalous stamens arising a third-way up the sepals.

Vouchers: *A. Bolus sub Guthrie 3939* (BOL); *Oliver & Oliver 11304* (NBG); *Esterhuysen 27443* (BOL); *Kotze 124* (NBG); *Phillips 2051* (SAM). Total number of specimens examined: 9.

30. **Lachnaea greytonensis** *Beyers*, sp. nov., *L. funicaulis* structura floris simili arte affinis, sed inflorescentia pseudobracteata, parte superiore hypanthii cyathiformi basi in tubo perangusto angustata, extra villoso-tomentosa, intra villoso-hirsuta, sepalis abaxialiter villoso-tomentosis.

TYPE.—Western Cape, 3419 (Caledon): Riviersonderend Mountains, Greyton, Boesmanskloof, jeep track to Die Galg, 640 m, (–BA), 12-11-1992, *Beyers 209* (NBG, holo.!; BOL!, K!, MO!, NY!, PRE!, S!, Z!, iso.).

Sparsely to much-branched, erect shrub up to 0.45 m tall, single-stemmed at base, corymbosely branched near ground; reseeder. *Branches* ascending to inclined, slender, terete, internodes $^3/_4$–$1^1/_2$ as long as leaves, felted, leafy, later becoming glabrous and naked without prominent leaf scars. *Leaves* decussate, adpressed, scattered, those below inflorescence crowded, sessile, epistomatic, narrowly elliptic, 2.8–4.5 × 0.8–1.2 mm, coriaceous, glabrous with villous-ciliate margin, later margins glabrous; adaxially obtusely concave or concave, dull, faintly white-punctulate; abaxially convex, smooth or subkeeled, glossy; apex rounded; base rounded; distal 2 leaf pairs subverticillate, broader than other leaves, bract-like, margin villous-ciliate; distal pair obovate, 2.9–3.5 × 1.9–2.3 mm, abaxially subkeeled, apex rounded or obtuse; subdistal pair obovate, 3.4–4.2 × 1.6–2.0 mm, abaxially keeled, apex acute or rounded. *Inflorescence* a terminal, sessile, 12–30-flowered, capitulum-like, pseudobracteate umbel with 1–5 open flowers at a time, 5–7 mm diam., on main and sometimes also on short lateral flowering branches just below main inflorescence forming a cluster of inflorescences at apex of main flowering branches; umbel appears to be enclosed at base by 2 pairs of involucral bracts but vegetative shoots were observed to develop in axils of distal bract-like leaf pair. *Flowers* ± actinomorphic, cream, pedi-

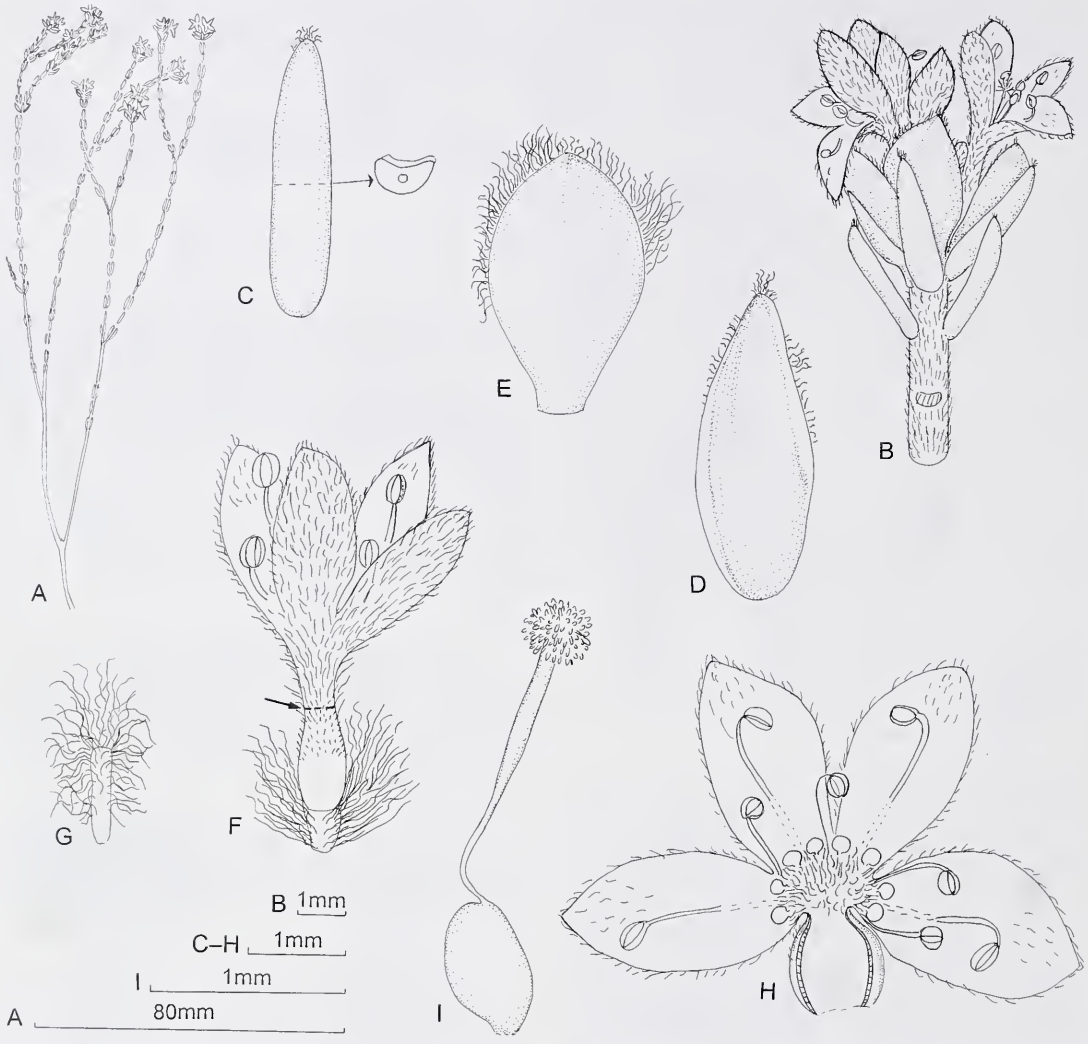

FIGURE 59.—*Lachnaea marlothii*, *Kotze 124* (NBG). A, portion of plant; B, flowering branch; C, leaf, abaxial view and c/s. D, E, bract-like leaves subtending inflorescence: D, from subdistal pair; E, from distal pair. F, H, flower: F, circumscission zone arrowed; H, l/s with gynoecium removed. G, elongated pedicel in fruiting stage; I, gynoecium. Scale bars: A, 80 mm; B–I, 1 mm.

cellate. *Pedicel* 0.5–2.7 mm long, villous, elongating in fruiting stage. *Hypanthium* 2.5–4.2 mm long, circumscissile $^1/_2$–$^1/_5$ from base; upper portion cup-shaped narrowing into a very short tube at base, villous-tomentose outside, inside villous-hirsute below floral scales, glabrous above; basal portion ellipsoid, outside distal $^1/_3$ tomentose, rest glabrous, inside glabrous. *Sepals* erect-patent, subequal, widely to very widely ovate, 0.8–1.3 × 0.8–1.3 mm, apex rounded or obtuse, adaxially glabrous or distal half villous-tomentose, abaxially villous-tomentose. *Stamens*: outer, antesepalous whorl exserted, arising at base of sepals or at rim of hypanthium; inner, antepetalous whorl enclosed or semi-exserted, arising a $^1/_3$–$^1/_3$ down upper portion of hyanthium; outer filaments 0.3–0.7 mm long, inner 0.2–0.7 mm long; anthers widely ellipsoid or spheroid, 0.3–0.4 mm long, abaxially without broad connective tissue. *Floral scales* enclosed, arising $^1/_2$–$^3/_4$ down upper portion of hypanthium, widely obovoid, 0.2–0.3 mm long, glabrous, white, later turning yellow in fresh state. *Ovary* narrowly obovoid or obovoid, 0.6–0.8 mm long, glabrous. *Style* terete-obconical, 0.8–2.2 mm long, glabrous. *Stigma* capitate or subcapitate, papillate (Figure 60).

Distribution and ecology

Only known from the Riviersonderend Mountains above Genadendal and Greyton in sandy soil at altitudes between 640 and 830 m (Figure 58). *Flowering time*: September to January.

Conservation status: Vulnerable (VU D2). This species has a restricted, localized distribution and being a reseeder, is vulnerable to frequent fires.

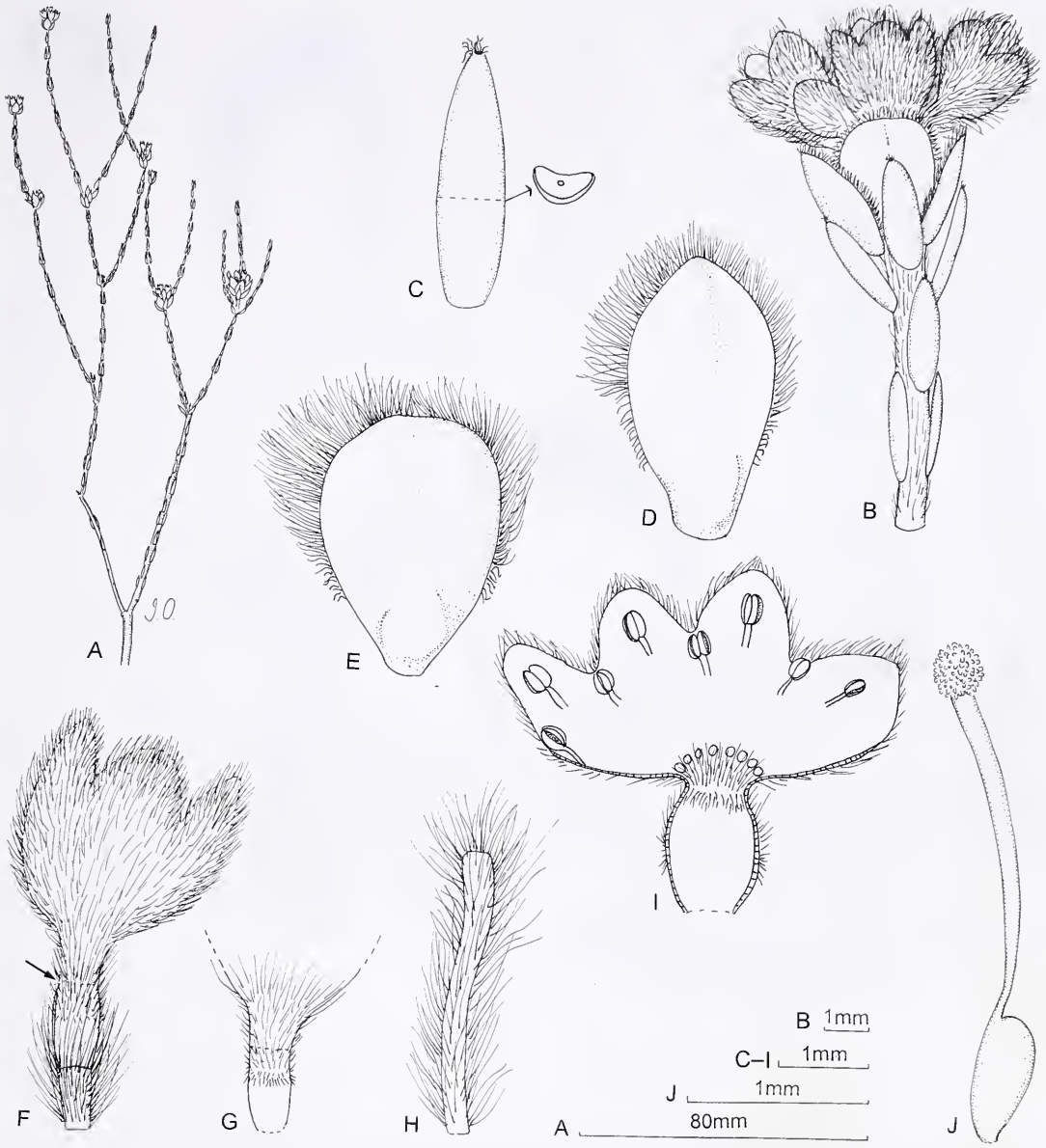

FIGURE 60.—*Lachnaea greytonensis*, *Beyers 209* (NBG). A, portion of plant; B, flowering branch; C, leaf, abaxial view and c/s. D, E, bract-like leaves subtending inflorescence: D, from subdistal pair; E, from distal pair. F, I, flower: F, circumscission zone arrowed; I, l/s with gynoecium removed. G, hypanthium; H, elongated pedicel in fruiting stage; J, gynoecium. Scale bars: A, 80 mm; B–J, 1 mm.

Diagnostic characters and relationships

This species is allied to *Lachnaea funicaulis* which has a similar flower structure but also differs in several aspects. *L. greytonensis* has a pseudobracteate umbel, the upper portion of the hypanthium is cup-shaped, narrowing into a very short tube at the base, which is villous-tomentose outside and villous-hirsute within, and the sepals are abaxially villous-tomentose. In *L. funicaulis* the umbel is bracteate, the upper portion of the hypanthium is funnel-shaped, tomentose-sericeous outside and adpressed hairy inside, and the sepals are abaxially tomentose-sericeous.

Etymology

The picturesque town of Greyton, which lies at the foot of the Riviersonderend Mountains, has prompted the specific epithet.

Vouchers: *Hansford 21* (NBG); *Kruger 1215* (NBG, PRE); *Stokoe 8031* (BOL), *9464* (BOL, PRE), *SAM58594*. Total number of specimens examined: 15.

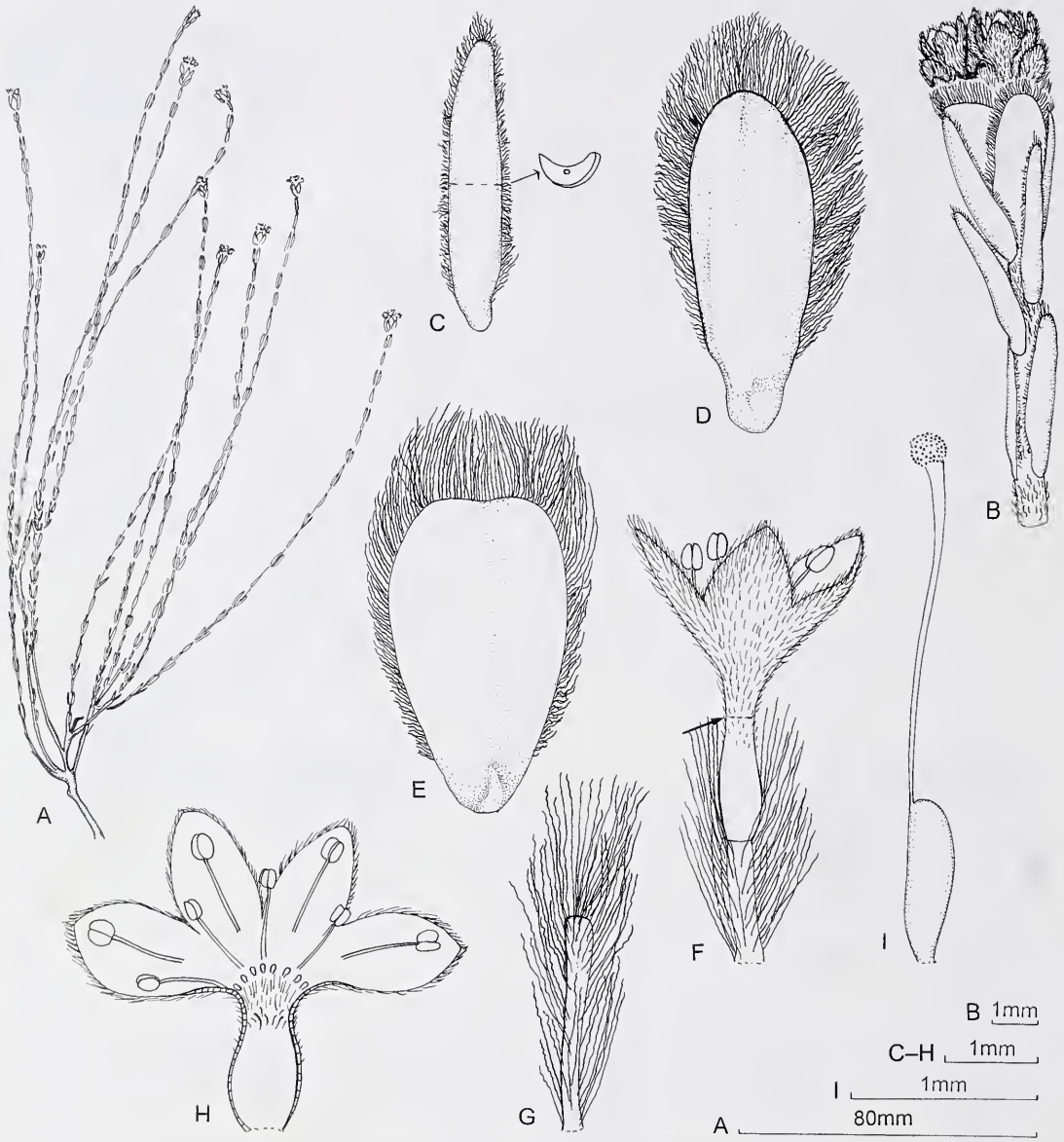

FIGURE 61.—*Lachnaea funicaulis*, *Bolus 53169* (NBG). A, portion of plant; B, flowering branch; C, leaf, abaxial view and c/s. D, E, involucral bracts: D, from subdistal pair; E, from distal pair. F, H, flower: F, circumscission zone arrowed; H, l/s with gynoecium removed. G, elongated pedicel in fruiting stage; I, gynoecium. Scale bars: A, 80 mm; B–I, 1mm.

31. **Lachnaea funicaulis** *Schinz* in Bulletin de l'Herbier Boissier 3: 408 (112) (1895); C.H.Wright: 25 (1915). Type: South Africa: in valley only in sand [Mostertshock], 3000 ft alt., 31-01-92, *Schlechter 401* (Z, holo.!; NY, iso.!).

Sparsely to moderately branched, erect shrub up to 0.45 m tall, single-stemmed at base, corymbosely branched near ground or higher up stem; reseeder. *Branches* erect, slender, terete, internodes as long as to one and a half times as long as leaves, felted, leafy, later glabrescent and naked without prominent leaf scars. *Leaves* decussate, adpressed, scattered, sessile, epistomatic, lanceolate, narrowly elliptic or narrowly obovate, 3.8–5.0 × 0.8–1.4 mm, coriaceous, glabrous with lanate-ciliate margin; adaxially concave, smooth, dull; abaxially convex, smooth or subkeeled, glossy; apex obtuse; base rounded. *Inflorescence* a terminal, sessile, bracteate, 8–12-flowered umbel with 3–6 open flowers at a time, 4–8 mm diam., on main and sometimes on short lateral flowering branches just below main inflorescence forming a cluster of inflorescences at apex. *Involucral bracts* 4, coriaceous, green, glabrous, margin brown, lanate-ciliate; inner pair obovate, 3–4 × 2.2–2.5 mm, apex truncate or sub-emar-

ginate; outer pair narrowly obovate or obovate, 3.5–4.6 × 1.8–2.5 mm, apex obtuse or truncate. *Flowers* subactinomorphic, cream, pedicellate. *Pedicel* 0.6–2.4 mm long, covered with long silky, ascending hairs, elongating in fruiting stage. *Hypanthium* 2.7–3.5 mm long, circumscissile ± $^1/_2$–$^1/_3$ from base; upper portion funnel-shaped, outside tomentose-sericeous but around circumscission zone puberulent, inside adpressed hairy; basal portion ellipsoid, outside glabrous except near circumscission zone puberulent, inside glabrous. *Sepals* erect-patent, subequal, shape variable, ovate to widely ovate, elliptic or obovate to widely obovate, 1.0–1.6 × 0.8–1.5 mm, apex rounded or obtuse, adaxially glabrous or at apex adpressed hairy, abaxially tomentose-sericeous. *Stamens* exserted, or only outer, antesepalous whorl exserted and inner, antepetalous whorl semi-exserted; outer whorl arising at base of sepals or rim of hypanthium; inner whorl arising a $^1/_4$–$^2/_3$ down upper portion of hypanthium; outer filaments 0.5–0.9 mm long, inner 0.4–0.6 mm long; anthers ellipsoid, 0.3–0.4 mm long, abaxially without broad connective tissue. *Floral scales* enclosed, arising $^1/_2$–$^4/_5$ down upper portion of hypanthium, narrowly ellipsoid or clavate, 0.2–0.3 mm long, glabrous. *Ovary* narrowly ellipsoid or narrowly ovoid, 0.6–1.6 mm long, glabrous. *Style* terete-obconical, 1.9–2.5 mm long, glabrous. *Stigma* either subcapitate and elongate-papillate or capitate and papillate (Figure 61).

Distribution and ecology

Recorded from the mountains east and south of Ceres in sandy or stony soil at altitudes between 500 and 1 000 m (Figure 62). *Flowering time*: July to March.

Conservation status: Vulnerable (VU D2). Only known from a few collections, most of which are old. This species has a restricted distribution and being a reseeder, is vulnerable to frequent fires.

Diagnostic characters and relationships

Lachnaea funicaulis can easily be confused with *L. villosa* as the habit and inflorescence structure are somewhat similar. However, the inflorescence, flower structure and indumentum of the two species are quite different. In *L. funicaulis* the inflorescence is bracteate, the upper portion of the hypanthium and the sepals are tomentose-sericeous on the outside, and the floral scales are enclosed, arising midway to four-fifths of the way down the upper portion of the hypanthium. *L. villosa*, on the other hand, has a pseudobracteate inflorescence, the upper portion of the hypanthium and the sepals are villous-tomentose on the outside and the floral scales, which arise in the mouth of the hypanthium, are exserted. It can be distinguished from its sister species, *L. oliverorum*, by having an 8–12-flowered umbel, smaller flowers (up to 5 mm long), a funnel-shaped hypanthium and by the sepals being tomentose-sericeous on the outside.

Vouchers: *Bolus 5316* (BOL, NBG, SAM), *HNAA1357* (BOL, NBG, PRE, S, Z); *Esterhuysen 26402* (BOL, PRE); *Hugo 2332* (NBG, PRE); *Rogers 17637* (GRA, PRE, Z); *Schlechter 9961* (BOL, PRE, S, Z). Total number of specimens examined: 32.

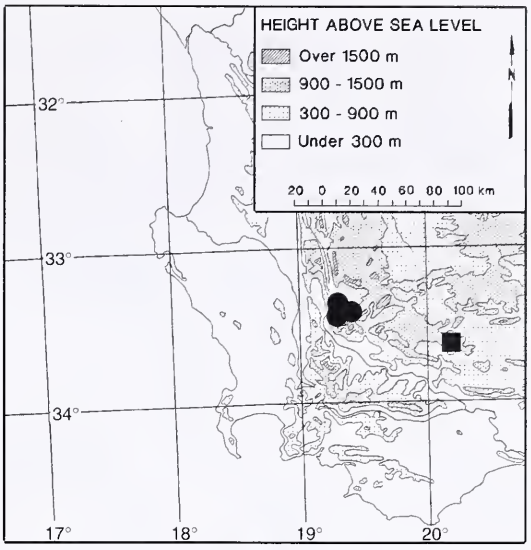

FIGURE 62.—Known distribution of *Lachnaea funicaulis*, ●; and *L. oliverorum*, ■.

32. **Lachnaea oliverorum** *Beyers*, sp. nov., *L. greytonensis* similis, sed differt inflorescentia bracteata, floribus duplo longioribus, parte superiore hypanthii cyathiformi basin versus in tubum decrescenti, verticillisque ambobus staminum exsertis.

TYPE.—Western Cape, 3320 (Montagu): Montagu District, Waboomsberg, east of Pypsteelfontein, on level, sandy area, 1 280 m, (–CA), 13-07-1994, *Oliver 10478* (NBG, holo.!; BOL!, K!, MO!, PRE, S!, iso.).

Sparsely to much-branched, erect shrub up to 0.5 m tall, single-stemmed at base; reseeder. *Branches* ascending to inclined, slender, terete, internodes a $^1/_3$ to twice as long as leaves, felted, leafy, later glabrescent and naked without prominent leaf scars. *Leaves* decussate, adpressed or ascending, scattered, sessile, narrowly elliptic or lanceolate, 3–5 × 0.8–1.5 mm, those below inflorescence crowded, ovate or elliptic, 3.2–5.4 × 1.8–2.2, coriaceous, glabrous with lanate-ciliate margin, later margins glabrous; adaxially obtusely concave or concave, dull, faintly white-punctulate; abaxially convex, smooth or subkeeled, glossy; apex rounded; base rounded. *Inflorescence* a terminal, sessile, 18–22-flowered, capitulum-like, bracteate umbel with 2–6 open flowers at a time, 8–15 mm diam., on main and also on short lateral flowering branches just below main inflorescence, forming a cluster of inflorescences at apex of main flowering branches. *Involucral bracts* 4, coriaceous, green or green with a maroon tinge, glabrous, margin lanate-ciliate; distal pair ovate or obovate, 5.3–7.0 × 3.3–3.9 mm, adaxially concave, abaxially convex, subkeeled in upper half, apex rounded; subdistal pair elliptic or obovate, 4.7–6.3 × 2.3–3.7 mm, adaxially concave, abaxially convex, subkeeled in upper half, apex acute or rounded. *Flowers* ± actinomorphic, cream, pedicellate. *Pedicel* 0.7–4.6 mm long, at first covered with long, ascending,

FIGURE 63.—*Lachnaea oliverorum*, *Oliver 10478* (NBG). A, portion of plant; B, flowering branch. C, D, leaf: C, abaxial view and c/s; D, leaf subtending inflorescence (abaxial view). E, F, involucral bracts: E, from subdistal pair; F, from distal pair. G, J, flower: J, l/s with gynoecium removed. H, hypanthium and circumscission zone arrowed; I, elongated pedicel in fruiting stage; K, gynoecium. Scale bars: A, 80 mm; B–K, 1 mm.

silky hairs later becoming villous, elongating in fruiting stage. *Hypanthium* 5.0–6.2 mm long, circumscissile a $^1/_4$–$^1/_3$ from base; upper portion cup-shaped narrowing into tube at base, villous outside, cup-shaped portion glabrous inside, tubular portion adpressed hairy; basal portion of hypanthium narrowly ellipsoid or narrowly obovoid, outside distal $^2/_3$ puberulent, rest glabrous, inside glabrous. *Sepals* erect-patent, subequal, ovate to widely ovate, 2.1–3.3 × 1.4–2.2 mm, apex rounded, adaxially glabrous in lower half, pilose in upper half, abaxially villous-tomentose. *Stamens* exserted; outer, antesepalous whorl arising near base of sepals or on rim of hypanthium; inner, antepetalous whorl arising $^1/_2$–$^2/_3$ down cup-shaped portion of upper portion of hypanthium; outer filaments 0.9–1.6 mm long, inner 0.8–1.7 mm long; anthers ellipsoid, 0.5–0.6 mm long, abaxially without broad connective tissue. *Floral scales* included, arising $^2/_3$–$^3/_4$ down cup-shaped portion of upper portion of hypanthium, widely obovoid or capitate, 0.4–0.6 mm long, glabrous, translucent white in fresh state. *Ovary* narrowly ellipsoid or ellipsoid, 0.9–1.4 mm long, glabrous. *Style* terete-obconical, 3.8–4.3 mm long, glabrous. *Stigma* subcapitate, elongate-papillate (Figure 63).

Distribution and ecology

Only known from Waboomsberg in the Montagu District where it grows in sandy soil at altitudes between 1 280 and 1 400 m (Figure 62). *Flowering time*: June to August.

Conservation status: Vulnerable (VU D2). This is a species with a very restricted distribution, and being a reseeder is vulnerable to frequent fires.

Diagnostic characters and relationships

Lachnaea oliverorum can be distinguished from its sister species, *L. funicaulis*, by having 18–22-flowered umbels, larger flowers (up to 9 mm long), a villous-tomentose indumentum on the flowers and the cup-shaped upper portion of the hypanthium. It superficially resembles *L. greytonensis*, a distant relative, which has a similar floral structure but differs in having bracteate inflorescences, larger flowers, the hypanthium above the circumscission zone which is cup-shaped in the upper half and narrows into a well-developed tube below, and in the exserted stamens.

Eponymy

This species is named after E.G.H. (Ted) and Inge Oliver, two of my colleagues, who have been a constant source of inspiration. They have always been on the look out for material of *Lachnaea* on their plant collecting trips.

Vouchers: *Oliver 10478* (BOL, K, MO, NBG, PRE, S); *Viviers & Vlok 430* (NBG, PRE); *Williams 1195* (NBG, PRE). Total number of specimens examined: 10.

33. **Lachnaea pendula** *Beyers*, sp. nov., distincta, inflorescentia parva, pendula, bracteata, pubescentiaque pallide aurea in pagina abaxiali sepalorum facile dignoscenda.

TYPE.—Western Cape, 3319 (Worcester): Worcester Dist., Fonteintjiesberg, Meiring's Plateau, on shaly slopes, 1 330–1 665 m, (–AD), 20-10-1963, *Esterhuysen 30420* (BOL, holo.!; S!, iso.).

Sparsely to moderately branched, erect to decumbent shrub up to 0.45 m tall, single-stemmed at base, branching near ground; reseeder. *Branches* ascending to patent, slender, terete, internodes $^2/_3$ to as long as leaves, felted or covered with adpressed long silky hairs admixed with crisped hairs, leafy, later glabrescent and naked without prominent leaf scars. *Leaves* decussate, adpressed, scattered, sessile, narrowly elliptic to elliptic or narrowly ovate to ovate, 1.8–2.4 × 0.6–0.8 mm, coriaceous, glabrous; adaxially concave, enervate, dull; abaxially convex, enervate or subkeeled, glossy; apex rounded, villous-tufted; base rounded. *Inflorescence* a terminal, sessile, pendulous, bracteate, up to ± 35-flowered umbel with 5–8 open flowers at a time, 3–5 mm diam., on main flowering branches. *Involucral bracts* 4, elliptic or obovate to widely obovate, 2.0–2.5 × 1.2–2.2 mm (distal pair always wider), coriaceous, green, glabrous; adaxially concave; abaxially convex, keeled in upper half; margin tinged brown in upper half, white-ciliate; apex rounded or obtuse. *Flowers* subactinomorphic, cream or pale yellow, pedicellate. *Pedicel* 0.5–1.5 mm long, villous, elongating in fruiting stage. *Hypanthium* 1.5–2.2 mm long, circumscissile $^2/_3$–$^4/_5$ from base; upper portion shortly funnel-shaped, sericeous outside, adpressed hirsute inside; basal portion ellipsoid or obovoid, outside pubescent in upper $^1/_3$–$^1/_2$, glabrous below, inside glabrous. *Sepals* patent, subequal, ovate or elliptic, 0.9–1.7 × 0.6–0.9 mm, apex subacute or rounded, adaxially glabrous, abaxially sericeous, pale gold-coloured. *Stamens* exserted; outer, antesepalous whorl arising at base of sepals; inner, antepetalous whorl arising at rim of hypanthium; outer filaments 0.6–0.9 mm long, inner 0.3–0.8 mm long; anthers widely ellipsoid or depressed spheroid, 0.2–0.3 mm long, abaxially without broad connective tissue. *Floral scales* exserted, arising in mouth of hypanthium near rim just below antepetalous stamens, narrowly obovoid or obovoid, 0.3–0.6 mm long, glabrous. *Ovary* ellipsoid or obovoid, 0.6–0.9 mm long, glabrous. *Style* terete-obconical, 1.1–1.3 mm long, sericeous in upper half, glabrous below. *Stigma* capitate, elongate-papillate (Figure 64).

Distribution and ecology

Lachnaea pendula has been recorded from the Skurweberg and Witsenberg northwest of Ceres and from the Hex River Mountains southeast of Ceres, on stony slopes at altitudes between 1 330 and 2 000 m (Figure 65). *Flowering time*: September to December.

Conservation status: Data Deficient (DD). Only known from a few herbarium collections from the

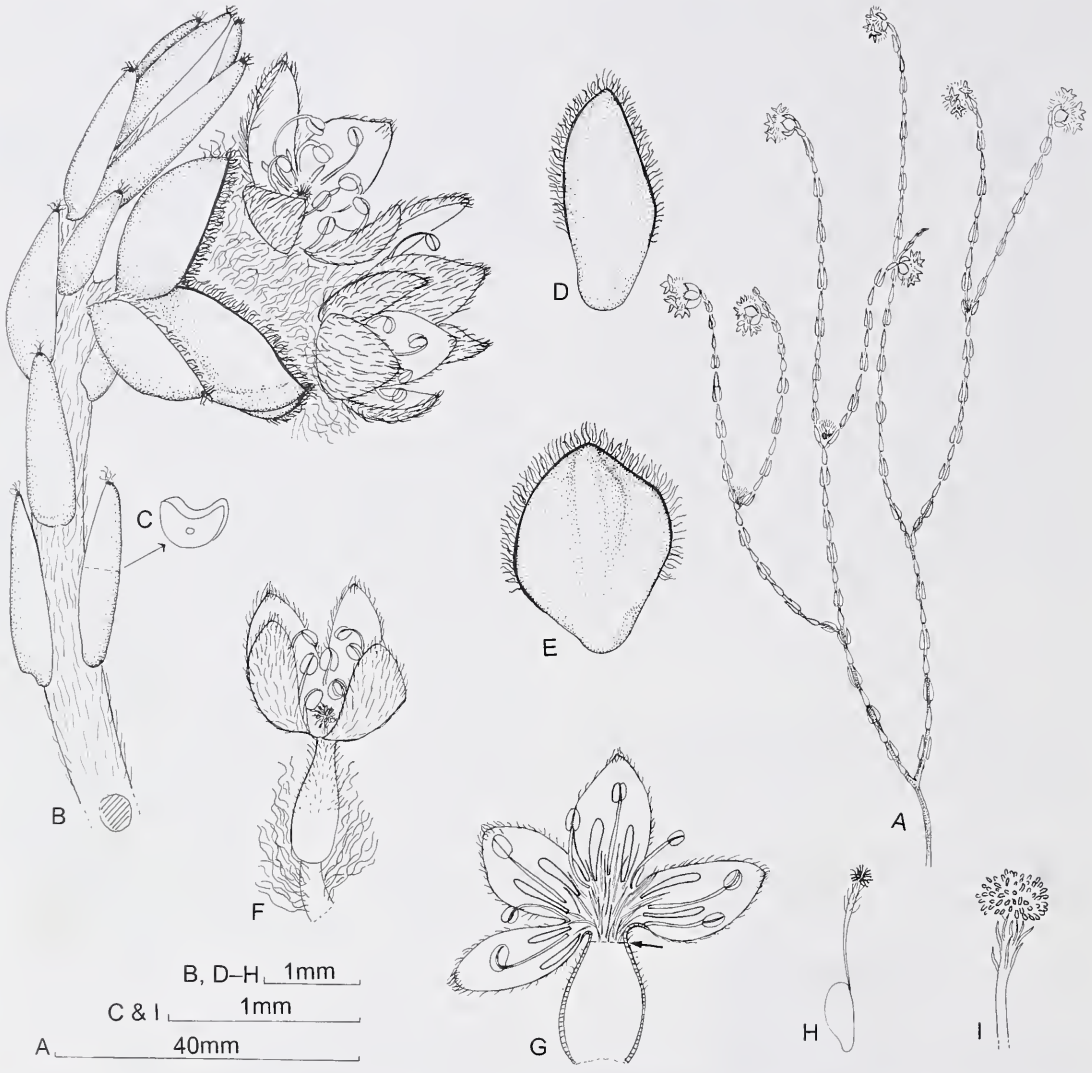

FIGURE 64.—*Lachnaea pendula*, *Esterhuysen 30420* (BOL). A, portion of plant; B, flowering branch; C, c/s leaf. D, E, involucral bracts: D, from subdistal pair; E, from distal pair. F, G, flower: G, l/s with gynoecium removed and circumscission zone arrowed. H, gynoecium; I, stigma and upper portion of style. Scale bars: A, 40 mm; B–I, 1 mm.

Worcester District by Esterhuysen, Stokoe and Andreae of which the most recent was collected in 1963.

Diagnostic characters and relationships

Lachnaea pendula is a sister species of *L. penicillata* based on two shared characters: inflorescence borne on the main flowering branches and a pubescent style. *L. pendula* can easily be distinguished by its small, pendulous, bracteate inflorescences and the pale gold-coloured pubescence on the abaxial side of the sepals.

Etymology

The specific epithet refers to the pendulous inflorescences.

Vouchers: *Andreae 1144* (NBG, PRE); *Esterhuysen 21858* (BOL), *29780* (BOL, S), *s.n.* (BOL); *Stokoe SAM58632*. Total number of specimens examined: 9.

34. **Lachnaea penicillata** *Meisn.* in Linnaea 14: 421 (1840); Meisn.: 579 (1857); C.H.Wright: 25 (1915). Type: between Sparrbosch and Tradouw, in rocky area, 2000–2500 ft. (IV. A.), *Drège s.n.* (NY, holo.!; P!, S!, SAM!, iso.).

Passerina filiformis L. var. *depauperata* E.Mey. ex Meisn.: 422 (1840) nom. nud. in synonymy.

Passerina brunniades Eckl. & Zeyh. (ex parte) ex Meisn.: 579 (1857) nom. nud. in synonymy.

Passerina brunioides Eckl. & Zeyh. (ex parte) ex Meisn.: 579 (1857) nom. nud. in synonymy.

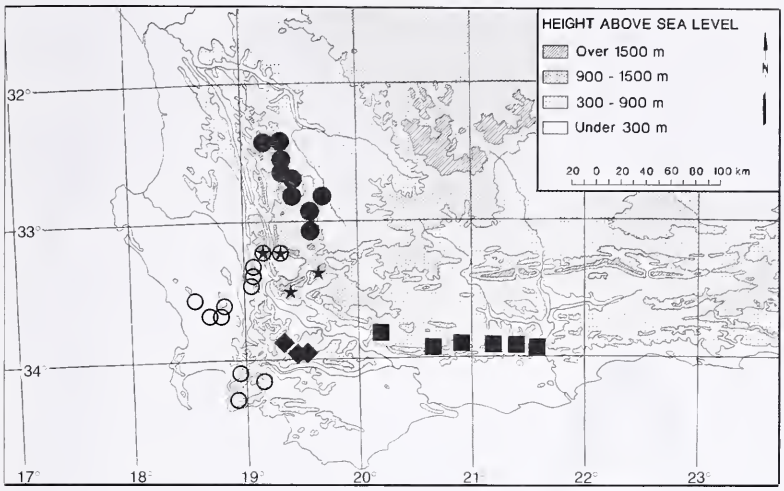

FIGURE 65.—Known distribution of *Lachnaea pendula*, ★; *L. pendula*, inexact localities, ☆; *L. penicillata*, ■; *L. eriocephala*, ○; *L. naviculifolia*, ●; and *L. rupestris*, ◆.

Lachnaea passerinoides N.E.Br.: 132 (1901); C.H.Wright: 25 (1915). Type: Cape Colony, Riversdale Division, on mountains of Garcia's Pass, alt. 1200 ft, *Galpin 4497* (K, holo.!; BOL!, iso.).

Compact, round, much-branched shrub up to 0.4 m tall, single-stemmed at base, corymbosely branched near ground, or multi-stemmed at base; reseeder or resprouter. *Branches* ascending or inclined, slender, lax, terete, internodes $^2/_3$–$^3/_4$ as long as leaves, felted, leafy, later glabrescent and naked without prominent leaf scars. *Leaves* decussate, adpressed, scattered, sessile, epistomatic, lanceolate or narrowly elliptic, 2.0–3.7 × 0.6–1.0 mm, coriaceous; adaxially concave, enervate, dull; abaxially convex, subkeeled or keeled, glossy, glabrous; margin lanate-ciliate, later glabrescent; apex obtuse, tufted; base rounded. *Inflorescence* a terminal, sessile, 3–12-flowered, bracteate umbel with a single open flower at a time, 3–4 mm diam., on main flowering branches. *Involucral bracts* 4, coriaceous, green; distal pair narrowly obovate or obovate, 3–4 × 1–2 mm; adaxially concave; abaxially convex, enervate or keeled, glabrous; margin scarious, brown, ciliate in upper half, lanate-ciliate in lower half; apex emarginate; subdistal pair narrowly elliptic or elliptic, 3–4 × 1.0–1.3 mm; adaxially concave; abaxially convex, keeled, glabrous; margin scarious, brown, lanate-ciliate or ciliate in upper half and lanate-ciliate in lower half; apex rounded. *Flowers* subactinomorphic, cream, pedicellate. *Pedicel* 0.5–2.0 mm long, covered with long silky, ascending hairs, elongating in fruiting stage. *Hypanthium* 2.2–3.0 mm long, circumscissile ± $^1/_2$ way from base; upper portion funnel-shaped, sericeous outside, adpressed hirsute inside; basal portion narrowly ellipsoid to elliptic or narrowly oblong to oblong, puberulent outside, glabrous inside. *Sepals* inclined, subequal, ovate, elliptic or obovate, 1.4–2.3 × 0.8–1.6 mm, apex rounded or obtuse, adaxially sparsely adpressed hairy, abaxially sericeous. *Stamens* exserted; outer, antesepalous whorl arising near base of sepals; inner, antepetalous whorl arising at rim of hypanthium; outer filaments 0.5–0.8 mm long, inner 0.4–0.7 mm long; anthers widely ellipsoid or spheroid, 0.3–0.4 mm long, abaxially without broad connective tissue. *Floral scales* exserted, arising immediately below antepetalous stamens in mouth of hypanthium, narrowly ellipsoid or narrowly obovoid, 0.5–0.7 mm long, glabrous, translucent white in fresh state. *Ovary* narrowly ellipsoid or ellipsoid, 0.6–1.0 mm long, glabrous. *Style* terete-obconical, 2.1–2.9 mm long, upper half covered with silky, ascending hairs, lower half glabrous. *Stigma* capitate, elongate-papillate (Figure 66).

Distribution and ecology

Lachnaea penicillata ranges from the Langeberg Mountains near Montagu in the west, eastwards to the Gourits River. It grows in sandy or stony clay soils at altitudes between 300 and 1 330 m (Figure 65). *Flowering time*: throughout the year.

Conservation status: Lower Risk Least Concern (LRlc).

Diagnostic characters and relationships

Lachnaea penicillata superficially resembles *L. fimicaulis*, but its inflorescence and flower structure differ. In *L. penicillata* the bracteate umbel, which has been interpreted as a single-flowered inflorescence in the past, produces one mature flower at a time; it protrudes beyond the involucral bracts. The immature flowers, fruits and pedicels remain tightly enclosed inside the involucral bracts. In *L. fimicaulis* the bracteate umbel has 3–6 mature (open) flowers at a time and the floral scales are enclosed, arising midway to four-fifths way down the upper portion of the hypanthium, whereas in *L. penicillata* they arise at the mouth of the hypanthium and are exserted.

Lachnaea penicillata is a sister species of *L. pendula* based on two shared characters: inflorescence borne on the main flowering branches and a pubescent style. It can easily be distinguished from *L. pendula* by the erect inflorescences and the leaf margins which are lanate-ciliate, later glabrescent.

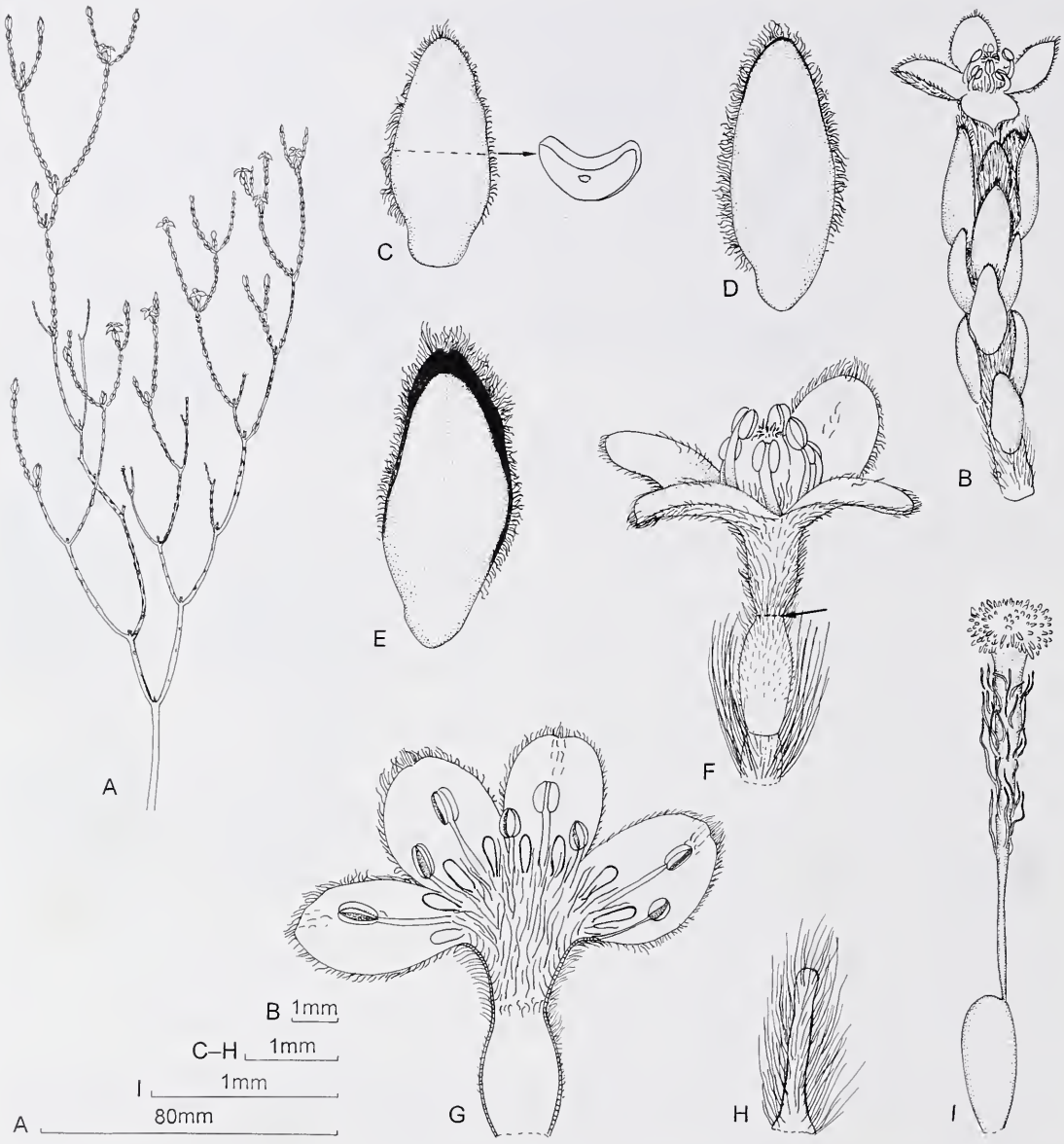

FIGURE 66.—*Lachnaea penicillata*, *Beyers 173* (NBG). A, portion of plant; B, flowering branch; C, leaf, abaxial view and c/s. D, E, involucral bracts: D, from subdistal pair; E, from distal pair. F, G, flower: F, circumscission zone arrowed; G, l/s with gynoecium removed. H, elongated pedicel in fruiting stage; I, gynoecium. Scale bars: A, 80 mm; B–I, 1 mm.

Vouchers: *Beyers 173* (K, MO, NBG, PRE, WU), *175* (K, MO, NBG, PRE); *Bolus 11372* (BOL, PRE); *McDonald 1251* (NBG, PRE), *1631* (K, MO, NBG, PRE, S), *1980* (K, MO, NBG, PRE, WU). Total number of specimens examined: 78.

35. **Lachnaea eriocephala** *L.*, Species plantarum, edn 1, 1: 560 (1753); L.: 514 (1762); Crantz: 128 (1766); Burm.f.: 12 (1768); Lam.: 374 (1792); Willd.: 434 (1799); Andrews: t. 104 (1800); C.F.Gaertn.: 195, t. 215 (1807); Sims: t. 1295 (1810); W.T.Aiton: 415 (1811); Loisel.: t. 234 (1820); Meisn.: 411 (1840); Meisn.: 575 (1857); C.H.Wright: 20 (1915). Type: Hottentots Holland Mtns, Sir Lowry's Pass, foot of pass, (–BB), *Beyers 270* (NBG, neo.!; BM!, BOL!, K!, MO!, NY!, P!, PRE!, S!, Z!, isoneo.). *Note*: no original material used by Linnaeus as basis for the name was found.

Passerina eriocephala (L.) Spreng.: 240 (1825); non Thunb. 75 (1794); non Thunb.: 375 (1823).

Passerina cephalophora Thunb.:75 (1794); Wikstr.: 321 (1818); Thunb.: 375 (1823). Type: *Thunberg sheet 9571* (UPS, holo. –NBG, photo.!; S [Herb. Montinii]!, iso.).

Lachnaea purpurea Andrews: t. 293 (1803); W.T.Aiton: 415 (1811); Sims: t. 1594 (1813); Wikstr.: 323 (1818); Lodd.: t. 273

(1818); C.H.Wright: 21 (1915). Type: Andrews, The botanist's repository: t. 293 (icono.!).

L. eriocephala L. var. *purpurea* (Andrews) Meisn.: 576 (1857).

Lachnaea rosea Baill.:108 (1880). Type: Baill., Natural history of plants 6, illustration [figs 74–76] on page 108 (icono.!).

Erect, sparsely to moderately branched shrub up to 0.6 m tall, single-stemmed at base; reseeder. *Branches* ascending, subrigid, terete, at first sericeous-hirtellous, later glabrescent, leafy, becoming naked with leaf scars. *Leaves* decussate, ascending or subadpressed, imbricate, sessile, epistomatic, coriaceous, lanceolate or narrowly elliptic, 5.2–15.0 × 1.0–2.5 mm, glabrous; adaxially flat to concave, enervate, white-punctulate, dull; abaxially convex and keeled, usually more so towards apex, glossy; margin at first ciliate, later glabrous; apex rounded or acute; base rounded; distal 2 or 3 leaf pairs subtending inflorescence bract-like, elliptic to widely elliptic, oblate, or obovate to very widely obovate, 5.2–17.0 × 3.6–14.0 mm (distal pair the broadest), coriaceous, green or green tinged maroon; adaxially concave, glabrous; abaxially convex, keeled in upper half, glabrous to sparsely adpressed hairy; margin membranous, ciliate; apex acuminate to mucronulate; base cuneate or obtuse. *Inflorescence* a terminal, sessile, pseudobracteate, more than 40-flowered, capitulum-like umbel with up to 30 open flowers at a time, 25–55 mm diam., on main flowering branches; umbel appears to be enclosed at base by 2 or 3 pairs of involucral bracts but vegetative shoots develop in axils of distal bract-like leaves, although branching usually occurs below subdistal pair of bract-like leaves. *Flowers* zygomorphic, cream or mauve, pedicellate. *Pedicel* linear, abaxially produced beyond insertion of flower, 2–6 mm long, elongating in fruiting stage, villous, responsible for woolly appearance of old inflorescence. *Hypanthium* 5.8–15.0 mm long, circumscissile ± $^1/_5$ from base, circumscission zone not clearly defined; upper portion narrowly funnel-shaped, sericeous-hirsute outside, sericeous inside; basal portion narrowly ovoid, puberulent or glabrescent outside, glabrous inside. *Sepals* patent, unequal, anterior and lateral ones directed outwards, anterior one elliptic, 6.2–10.3 × 2.5–4.8 mm, lateral ones elliptic, 4.5–9.5 × 1.7–3.5 mm, posterior one ovate, 2.3–5.5 × 1.2–3.0 mm, always shorter than other three, adaxially sparsely sericeous, abaxially sericeous, apex rounded. *Stamens* exserted; outer, antesepalous whorl arising at or near base of sepals; inner, antepetalous whorl arising at rim of hypanthium, shorter than outer whorl; outer filaments 1.2–4.5 mm long, inner 1–3 mm long; anthers ellipsoid, 0.7–1.2 mm long, abaxially without broad connective tissue. *Floral scales* exserted, arising at mouth of hypanthium immediately below antepetalous stamens, obscured by hairs in mouth, linear, 0.6–1.0 mm long, glabrous, translucent white in fresh state. *Ovary* narrowly ovoid or ellipsoid, 1–2 mm long, glabrous. *Style* linear, 5.2–10.5 mm long, sericeous in upper half to three-quarters. *Stigma* brush-like (Figure 67).

Distribution and ecology

Lachnaea eriocephala has been recorded from the Roodezand, Obiekwa and Voëlvlei Mountains near Tulbagh, as far west as Dassenberg near Malmesbury and southwards to Betty's Bay at altitudes between 100 and 500 m (Figure 65). The locality information on the collection by Thunberg from the hot water springs in the Swartberg at Caledon is probably incorrect. No other collections have been made in this area. In the vicinity of Tulbagh the flowers are predominently mauve, rarely cream, whereas southwards all the plants have cream flowers. *Flowering time*: July to November.

Conservation status: Lower Risk Least Concern (LRlc).

Diagnostic characters and relationships

Lachnaea eriocephala is distinguished from the other species that have large, showy inflorescences with zygomorphic flowers, by the decussate, imbricate, lanceolate to narrowly elliptic leaves, which are abaxially keeled, and by the pedicels which are abaxially produced beyond the point of the flower attachment. It is easily distinguished from the species with the latter type of pedicels, by the strongly zygomorphic flowers.

Vouchers: *Beyers 238* (BOL, K, MO, NBG, PRE); *Bolus 5553* (BOL, GRA, PRE, SAM, Z); *Boucher 1885* (NBG, PRE); *Esterhuysen 18794* (BOL, NBG, PRE); *Rugge s.n.* (K, NBG, PRE); *Schlechter 1128* (GRA, SAM, Z). Total number of specimens examined: 121.

36. **Lachnaea naviculifolia** *Compton* in Journal of Botany 72: 21 (1934b). Type: Cape Province, Ceres Div., precise locality unknown. Exhibited at Ceres Wild Flower Show, October 1932, *Compton 4158* (BOL, holo.!; K, iso.!).

Erect, sparsely to moderately branched shrub up to 1.5 m tall, multistemmed at base; resprouter. *Branches* ascending, slender, terete, internodes $^1/_4$–$^2/_3$ as long as leaves, puberulent to sericeous below inflorescence [± 6 pairs of distal leaves], below glabrous or occasionally covered with short adpressed hairs, leafy, becoming naked with prominent leaf scars. *Leaves* decussate, ascending, erect or with apex turned inward, scattered, those below inflorescence crowded, sessile, epistomatic, glaucous, navicular, narrowly elliptic to elliptic, occasionally narrowly ovate to ovate, 7.5–16.0 × 1.5–5.5 mm, coriaceous or subfleshy, glabrous; adaxially obtusely concave, enervate, white-punctulate, dull; abaxially obtusely convex, enervate, glossy or dull; margin inflexed; apex rounded; base rounded; distal 3 pairs below inflorescence becoming gradually larger upward and bract-like, winged, elliptic to very widely elliptic or obovate to very widely obovate, 6.0–21.5 × 4–13 mm, coriaceous, glaucous or green tinged red, greeny yellow tinged red or reddish; adaxially concave; abaxially convex, subkeeled towards the apex, glabrous or adpressed hairy at apex; margin membranous, ciliolate, more so in upper half; apex cuspidate or mucronate; base rounded or cuneate. *Inflorescence* a terminal, sessile, more than 20-flowered, pseudobracteate, capitulum-like umbel with 8–15 open flowers at a time, 18–35 mm diam., usually only on main flowering branches; ebracteate umbel appears to be enclosed at base by 2 or 3 pairs of involucral bracts but vegetative shoots develop in axils of these bract-like leaves, although generally branching

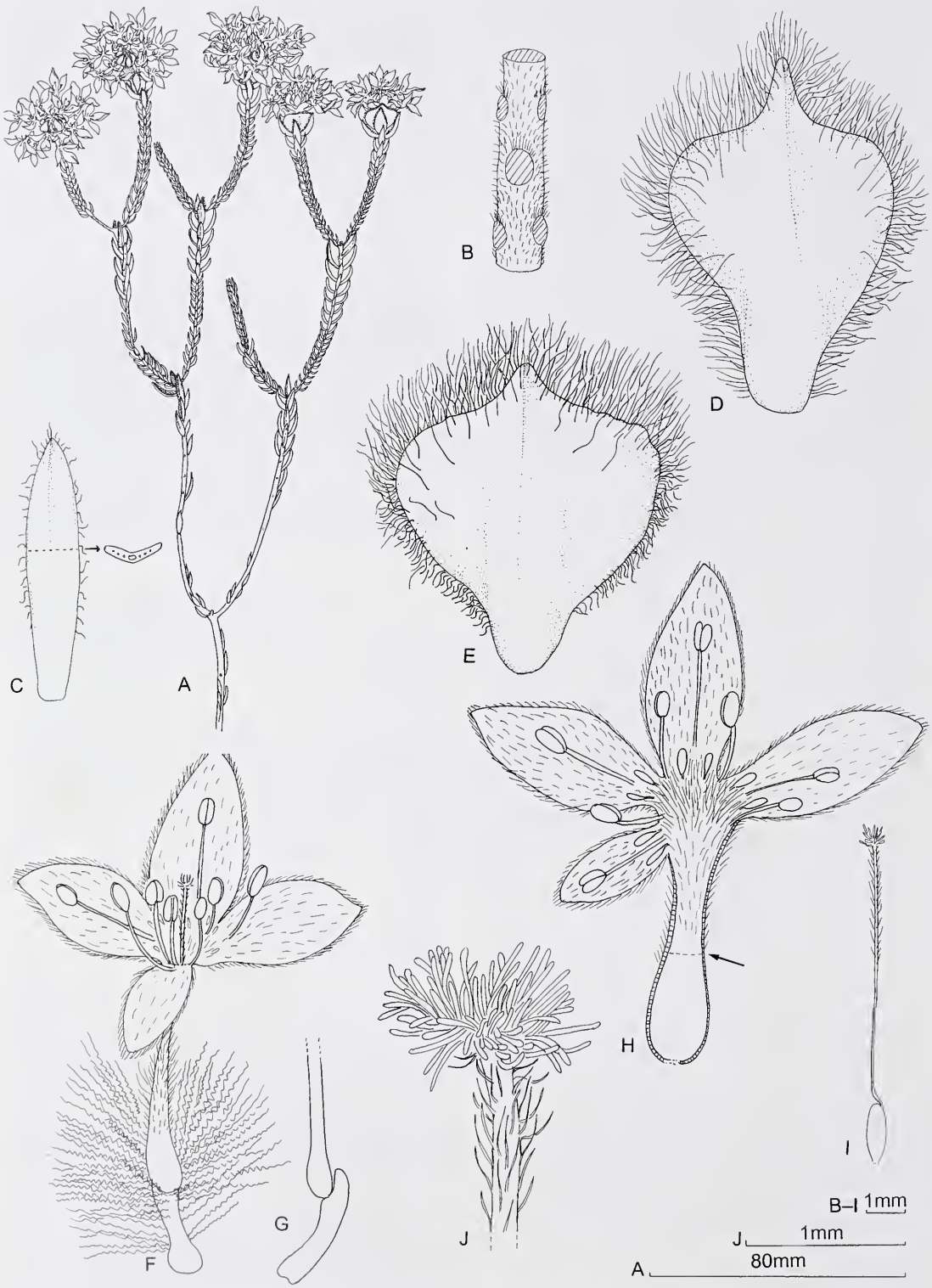

FIGURE 67.—*Lachnaea eriocephala, Beyers 54* (NBG). A, portion of plant; B, branch with leaves removed; C, leaf, abaxial view and c/s. D, E, bract-like leaves subtending inflorescence: D, from subdistal pair; E, from distal pair. F, H, flower: H, l/s with gynoecium removed and circumscission zone arrowed. G, pedicel abaxially produced beyond point of attachment of flower (lateral view); I, gynoecium; J, stigma and upper portion of style. Scale bars: A, 80 mm; B–J, 1 mm.

occurs below subdistal pair of bract-like leaves. *Flowers* subactinomorphic, white or white tinged pink or mauve, or cream, pale pink, pale blue, pale yellow or yellowish green, scented. *Pedicel* dorso-ventrally flattened, abaxially produced beyond point of attachment of flower, rectangular, 2.0–4.5 mm long, elongating in fruiting stage, adaxially villous, abaxially sericeous. *Hypanthium* 7–13 mm long, circumscissile $^1/_5$–$^2/_5$ from base; upper portion narrowly funnel-shaped, sericeous on both sides; basal portion ellipsoid or obovoid, outside puberulent in upper $^1/_3$, rest glabrous, inside glabrous. *Sepals* patent, ± equal or occasionally subequal, adaxially glabrous or occasionally sparsely sericeous along midvein, abaxially sericeous, elliptic, rounded to obtuse, anterior one 4–8 × 2.2–4.0 mm, lateral ones 3.4–6.2 × 2–4 mm, posterior one 3.6–6.5 × 1.6–3.8. *Stamens* exserted; outer, antesepalous whorl arising at base of sepals; inner, antepetalous whorl arising at rim of hypanthium, shorter than outer whorl; outer filaments 3.0–5.5 mm long, inner 1.4–3.5 mm long; anthers oblong or ellipsoid to widely ellipsoid, 0.6–1.3 mm long, abaxially with broad connective tissue. *Floral scales* exserted, arising at mouth of hypanthium immediately below antepetalous stamens, linear, 0.8–2.0 mm long, glabrous, translucent white in fresh state. *Ovary* ellipsoid or obovoid, 1.6–2.4 mm long, glabrous. *Style* terete-obconical, 8.0–14.5 mm long, sericeous in upper half. *Stigma* brush-like (Figure 68).

Distribution and ecology

Lachnaea naviculifolia ranges from the central Cederberg in the north, along the eastern side of the Cold Bokkeveld to as far south as Watervalsberg at altitudes between 1 000 and 1 865 m, and occurs in sandy, flat areas and on steep, rocky slopes (Figure 65).

Both narrow- and broad-leaved forms occur. Plants with usually narrow leaves occur in the central Cederberg. Around Sneeuberg and Kromrivier both leaf forms occur, whereas southwards the leaves are broader and slightly succulent. *Flowering time*: August to November.

Conservation status: Lower Risk Least Concern (LRlc).

Diagnostic characters and relationships

Lachnaea naviculifolia is allied to *L. eriocephala*. Both have the derived character state of pedicels abaxially produced beyond the flower attachment. *L. naviculifolia* is easily distinguished from *L. eriocephala* by the glaucous, naviculoid (boat-shaped) leaves, more or less regular flowers, rectangular pedicels which are dorso-ventrally flattened and the linear floral scales which are not obscured by hairs in the mouth of the hypanthium.

Vouchers: *Andrag 105* (NBG, PRE); *Esterhuysen 8109* (BOL, NBG), *30299* (BOL, S); *Le Maitre 328* (NBG, PRE); *Oliver 8062* (NBG, PRE), *9038* (NBG, PRE). Total number of specimens examined: 76.

37. **Lachnaea rupestris** *Beyers*, sp.nov., a *L. marlothii* pubescentia sparsa ramorum, foliis glabris, pedicellis dorso-ventraliter complanatis et abaxialiter ultra affixionem florum prolongatis, staminibus antesepalis basi sepalorum insertis, squamis anguste ellipsoideis vel anguste obovoideis dignoscenda.

TYPE.—Western Cape, 3319 Stettynsberg, southwestern slopes, (–CD), *Esterhuysen 11102* (BOL, holo.!; PRE!, iso.).

Low, straggling, moderately branched shrub up to 0.2 m tall, single-stemmed at base branching near ground; reseeder. *Branches* ascending to patent, slender, terete, internodes $^1/_3$ to as long as leaves, clothed with short crisped hairs admixed with short, retrorse ones, leafy, later glabrescent and naked without prominent leaf scars. *Leaves* decussate, subadpressed or ascending, scattered, sessile, epistomatic, lanceolate or narrowly elliptic, 3.0–5.4 × 0.6–1.0 mm, coriaceous; adaxially concave, enervate, dull; abaxially convex, often subkeeled in upper half, glossy, glabrous; apex rounded or subacute; base rounded; distal 2 leaf pairs subverticillate, partially enclosing inflorescence, broader than other leaves, bract-like, coriaceous, green or green with maroon tinge, glabrous; adaxially concave; abaxially convex keeled in upper half; elliptic to widely elliptic or obovate to widely obovate, 3.2–5.0 × 1.6–2.9 mm; margin ciliate; apex mucronulate or acute. *Inflorescence* a terminal, sessile, 12–22-flowered, pseudobracteate umbel with 3–5 open flowers at a time, 5–7 mm diam., on main flowering branches or also on a few, short, lateral branches immediately below main inflorescence forming a compact glomerule at apex of main flowering branch; umbel appears to be enclosed by 2 pairs of involucral bracts with ciliate margin, but vegetative shoots develop in axils of these bract-like leaves, although new shoots mostly arise from axils of subdistal pair of bract-like leaves. *Flowers* subactinomorphic, mauve or cream with mauve tinge, pedicellate. *Pedicel* dorso-ventrally flattened, abaxially produced beyond point of attachment of flower (more noticeable in fruiting stage), oblong, 0.4–1.2 mm long, slightly elongating in fruiting stage, villous. *Hypanthium* 2.0–2.5 mm long, circumscissile $^2/_3$–$^1/_2$ from base; upper portion funnel-shaped, sericeous outside, adpressed hirsute inside; basal portion ellipsoid, outside for most part glabrous but in vicinity of circumscission zone puberulous, inside glabrous. *Sepals* patent, subequal, ovate to elliptic, 1.6–1.9 × 0.8–1.4 mm, apex subacute or rounded, adaxially sparsely adpressed hairy or glabrous, abaxially sericeous. *Stamens* exserted; outer, antesepalous whorl arising at base of sepals; inner, antepetalous whorl arising on rim of hypanthium, shorter than outer whorl; outer filaments 1.0–1.2 mm long, inner 0.7–0.9 mm long; anthers widely ellipsoid to spheroid, 0.3–0.4 mm long, abaxially without broad connective tissue. *Floral scales* exserted, arising immediately below antepetalous stamens in mouth of hypanthium, narrowly obovoid or narrowly ellipsoid, 0.4–0.6 mm long, glabrous. *Ovary* ellipsoid, ± 1.0 mm long, glabrous. *Style* terete-obconical, 1.9–2.2 mm long, covered with silky ascending hairs in upper half. *Stigma* brush-like (Figure 69).

FIGURE 68.—*Lachnaea naviculifolia*, *Forsyth 525* (NBG). A, portion of plant. B, C, leaves: B, abaxial view and c/s; C, adaxial view. D, E, bract-like leaves subtending inflorescence: D, from subdistal pair; E, from distal pair. G, pedicel abaxially produced beyond point of attachment of flower (lateral view). F, H, flower: F, circumscission zone arrowed; H, l/s with gynoecium removed. I, gynoecium; J, stigma and upper portion of style. Scale bars: A, 80 mm; B–J, 1 mm.

Distribution and ecology

Lachnaea rupestris is known from the Stettynsberg north of Villiersdorp to the Riviersonderend Mountains above Genadendal, where it grows in rocky places at altitudes above 1 500 m (Figure 65). *Flowering time*: October to December.

As I have not seen this species in the wild, the description is based solely on herbarium specimens.

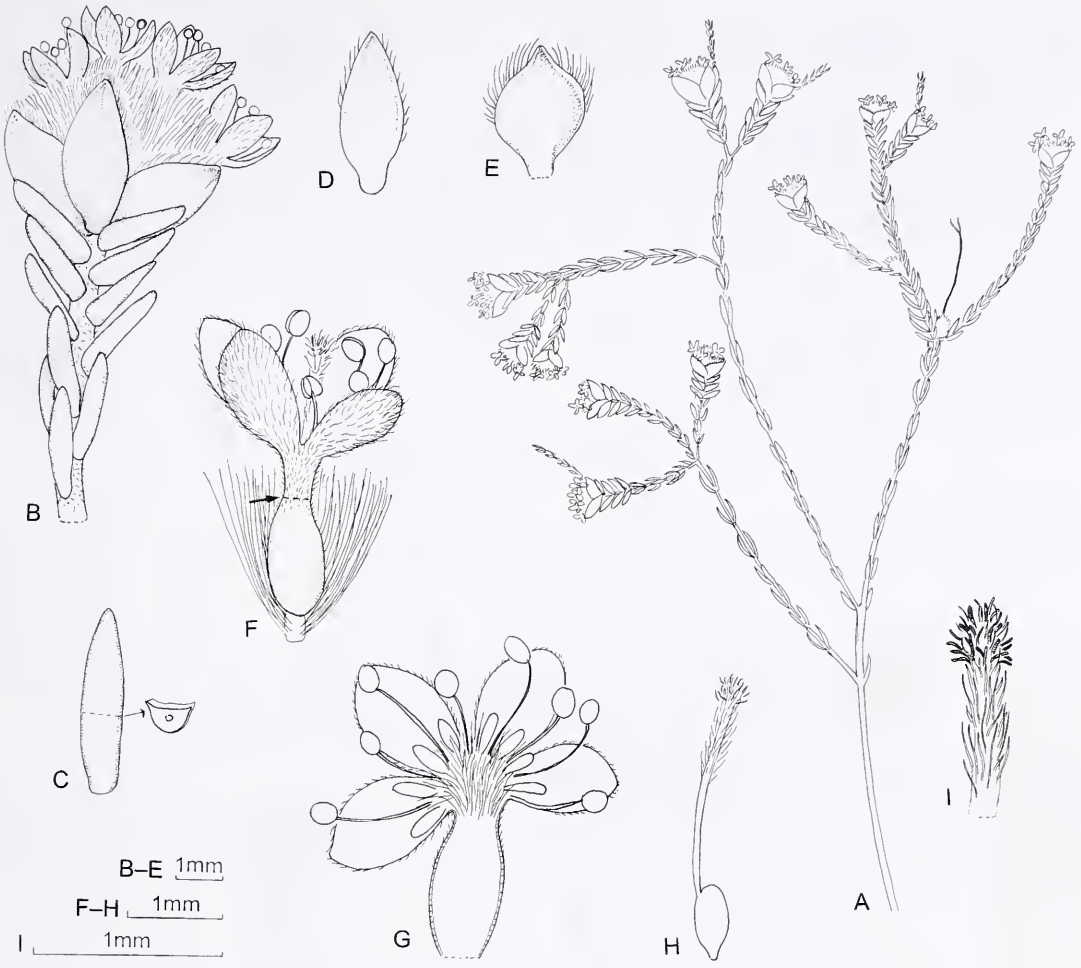

FIGURE 69.—*Lachnaea rupestris*. *Esterhuysen 11102* (BOL). A, portion of plant (life size); B, flowering branch; C, leaf, abaxial view and c/s. D, E, bract-like leaves subtending inflorescence: D, from subdistal pair; E, from distal pair. F, G, flower: F, circumscission zone arrowed; G, l/s with gynoecium removed. H, gynoecium; I, stigma and upper portion of style. Scale bars: B–I, 1 mm.

Conservation status: Vulnerable (VU D2). Only known from a few localities, and being a reseeder, it is vulnerable to frequent fires.

Diagnostic characters and relationships

Lachnaea rupestris is allied to *L. eriocephala* and *L. naviculifolia*, but is easily distinguished by its low straggling habit. It is superficially very similar to *L. marlothii* from which it can be distinguished by the thin pubescence of the branches, glabrous leaves, dorso-ventrally flattened pedicels, which are abaxially produced beyond the point of attachment of the flower, by the antesepalous stamens which arise at the base of the sepals and by the narrowly ellipsoid or narrowly obovoid floral scales.

Etymology

The rocky habitat favoured by this species has prompted the specific epithet, which means rock-dwelling.

Vouchers: *Esterhuysen 11102* (BOL, PRE); *Oliver 11262* (K, NBG, PRE), *s.n.* (NBG); *Stokoe 2524* (BOL), *2533* (PRE). Total number of specimens examined: 8.

38. **Lachnaea globulifera** *Meisn.* in Linnaea 14: 412 (1840); Meisn.: 576 (1857); C.H.Wright: 24 (1915). Type: in sandflats near Goudini, alt. 800–1200 ft (IV. B. b.), *Drège s.n.* (NY, holo.!; K!, P!, S!, SAM!, iso.).

Gonophylla setosa Eckl. & Zeyh. ex Meisn.: 576 (1857) nom. nud. in synonymy.

Two subspecies are recognized on the basis of regeneration strategy, indumentum of the branches and geographic separation. The diagnostic characters and relationships of the species are discussed under the typical species.

38a. subsp. **globulifera**

Slender, erect, sparsely to moderately branched shrub up to 0.6(–0.9) m tall, single-stemmed at base; reseeder.

FIGURE 70.—*Lachnaea globulifera* subsp. *globulifera*, *Beyers 240* (NBG): A, flowering branch. B, C, leaf: B, abaxial view and c/s; C, bract-like leaf from pair subtending inflorescence. D, involucral bract; F, pedicel abaxially produced beyond point of attachment of flower (lateral view); E, G, flower: E, circumscission zone arrowed; G, l/s with gynoecium removed. H, gynoecium; I, stigma and upper portion of style. *L. globulifera* subsp. *incana*, *Brown 575* (NBG): J, portion of plant. Scale bars: A–I, 1 mm; J, 80 mm.

Branches ascending, slender, wiry or semi-rigid, internodes $^1/_4$–$1^1/_2$ as long as leaves, terete, at first covered with short, crisped hairs, later glabrescent, leafy, becoming naked without prominent leaf scars. *Leaves* (excluding bract-like leaf pair subtending inflorescence) decussate, adpressed or ascending, scattered, sessile, epistomatic, narrowly elliptic or lanceolate, 5.4–12.0 × 0.7–1.7 mm, coriaceous, glabrous; adaxially obtusely concave to concave, enervate, ± white punctulate, dull; abaxially convex, subkeeled, glossy; apex acute to mucronate, sometimes tinged red; base rounded; those below inflorescence gradually wider to 2.5 mm wide, apex acuminate, margin occasionally ciliate; bract-like leaf pair subtending inflorescence narrowly elliptic to widely elliptic, ovate or obovate, 3.5–6.8(–10.0) × 1.7–3.5(–6.0) mm, coriaceous, green with maroon tinge, glabrous; margin membranous, ciliate; apex acute to acuminate; base attenuate. *Inflorescence* a terminal, sessile, bracteate, ± 50-flowered, capitulum-like umbel with up to 14 open flowers at a time, 5–20(–25) mm diam., on main flowering branches and also on a few short lateral branches immediately below main inflorescence, forming a compact glomerule; bracteate umbel appears to be enclosed at base by 2 pairs of involucral bracts but only 1 pair immediately below flowers may be regarded as being true bracts, as vegetative shoots develop in axils of subdistal pair. *Involucral bracts* 2, widely elliptic to widely obovate, 4.5–6.0(–10.0) × 2.3–4.5(–7.0) mm, coriaceous, green with maroon tinge, glabrous, adaxially concave, abaxially convex, keeled, margin membranous, ciliate, apex acute, mucronate or acuminate. *Flowers* ± actinomorphic, cream, cream with pink tinge or pale mauve, others cream turning mauve with age, unscented, pedicellate. *Pedicel* dorso-ventrally flattened, oblong to linear, abaxially elongated beyond insertion of flower, 0.3–2.2 mm long, elongating in fruiting stage, densely villous. *Hypanthium* 2.2–3.6(–7.0) mm long, circumscissile $^1/_4$–$^1/_2$ from base;

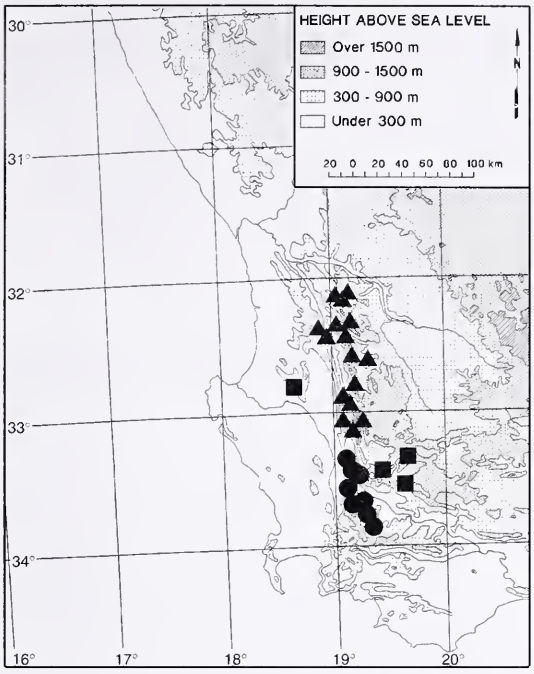

FIGURE 71.—Known distribution of *Lachnaea globulifera* subsp. *globulifera*, ●; *L. globulifera* subsp. *incana*, ▲; *L. montana*, ■.

upper portion narrowly funnel-shaped, sericeous outside, inside adpressed hirsute; basal portion ovoid to obovoid, outside puberulent in upper $^1/_3$–$^4/_5$, glabrous below, inside glabrous. *Sepals* patent, ± equal, adaxially sparsely sericeous or glabrescent, abaxially sericeous, elliptic to widely elliptic, ovate to widely ovate or widely obovate, 1.5–3.5(–4.5) × 1.3–2.5 mm, rounded. *Stamens* exserted, outer, antesepalous whorl arising at base of sepals, ± length of sepals, inner, antepetalous whorl arising at rim of hypanthium, shorter than outer whorl; outer filaments 1.3–3.0 (–4.4) mm long, inner 0.8–2.1(–3.5) mm long; anthers oblong to spheroid, 0.3–0.4(–0.8) mm long, abaxially without broad connective tissue. *Floral scales* exserted, arising at mouth of hypanthium immediately below antepetalous stamens, obscured by hairs in mouth, filiform, 0.2–0.6 mm long, glabrous, translucent in fresh state. *Ovary* narrowly obovoid or narrowly ellipsoid to ovoid, 0.8–1.5 mm long, glabrous. *Style* filiform, 1.7–4.0(–8.0) mm long, adpressed hairy in upper half to upper three-quarters. *Stigma* brush-like (Figure 70).

Distribution and ecology

Lachnaea globulifera subsp. *globulifera* has been recorded from the lower mountain slopes and flats of the Wintershoek Mountain north of Tulbagh southwards through Bainskloof to Du Toit's Kloof and southeast to Stettyn Mountain near Villiersdorp. It grows in sandy or sandy, stony soil at altitudes between 200 and 1 100 m (Figure 71). *Flowering time*: July to November and occasionally in January, February and May.

Conservation status: Lower Risk Least Concern (LRlc). Being a reseeder, frequent fires may impact negatively on this species.

Diagnostic characters and relationships

Lachnaea globulifera is allied to *L. montana* and *L. pedicellata* based on the following shared characters: inflorescence borne on main flowering branches and on short lateral flowering branches and the bracteate umbel with 2 involucral bracts, which is subtended by 2 bract-like leaves. It differs from *L. montana* by the ciliate involucral bracts, the smaller flowers and the filiform floral scales obscured by hairs in the mouth of the hypanthium. It is distiguished from *L. pedicellata* by the ciliate involucral bracts, the densely villous, oblong to linear pedicels and the filiform floral scales obscured by hairs in the mouth of the hypanthium.

Vouchers: *Beyers 253* (BOL, K, MO, NBG, PRE); *Bolus 5259* (BOL, Z); *Haynes 108* (NBG, PRE); *Hutchinson 398* (BOL, K, PRE); *Oliver 9903* (K, NGB, PRE); *Schlechter 1393* (GRA, K, PRE, S, Z). Total number of specimens examined: 77.

38b. subsp. **incana** *Beyers*, subsp. nov., a subsp. *globulifera* habitu repullulante, ramulis incanis, distributione magis septentrionali differt.

TYPE.—Western Cape, 3219 (Wuppertal): Citrusdal, Middelberg, stony, sandy soil against a rocky incline, (–CA), 3-11-1997, *Hanekom 2939* (NBG, holo.!; BOL!, K!, MO!, NY!, PRE!, S!, Z!, iso.).

L. globulifera var. *coerulescens* Eckl. & Zeyh. ex Meisn.: 576 (1857); C.H.Wright: 24 (1915). Type: [80] *Gonophylla coerulescens* [Clanwilliam, mountains at Brakfontein, July = 76.7], *Ecklon & Zeyher s.n.* (NY, holo.!; S!, SAM!, Z!, iso.).

Slender, erect or decumbent shrub, 0.3–0.6(–1.0) m tall, single-stemmed or multistemmed at base; resprouter. *Branches* felted, the older glabrescent, internodes $^1/_2$–$^3/_4$ length of leaves. *Leaves* scattered, narrowly elliptic to lanceolate, 4.4–7.3 × 0.9–1.7 mm; bract-like leaf pair subtending bracteate inflorescence ovate to elliptic, 3.7–5.3 × 1.9–3.5 mm, glabrous or towards abaxial margins adpressed pilose. *Inflorescence* 5.0–20.0 mm diam. *Involucral bracts* ovate to elliptic to widely elliptic, 4.0–5.7 × 2.0–3.7 mm, glabrous or towards abaxial margin adpressed pilose. *Hypanthium* 3.2–4.5 mm long, circumscissile $^2/_5$–$^3/_5$ from base, basal portion outside puberulent in upper half, trichomes variable, ellipsoid to ± clavate or acicular as in upper portion. *Sepals* ovate, elliptic to widely elliptic or rotund, 2.6–3.8 × 1.7–2.7 mm, apex acute, rounded or obtuse. *Ovary* ovoid to obovoid, 0.8–1.2 mm long.

Distribution and ecology

The known distribution of *L. globulifera* subsp. *incana* extends from the Pakhuis Mountains in the north near Clanwilliam southwards to the Agter Witzenberg Flats in the Ceres District. It seems to occur in sandy or

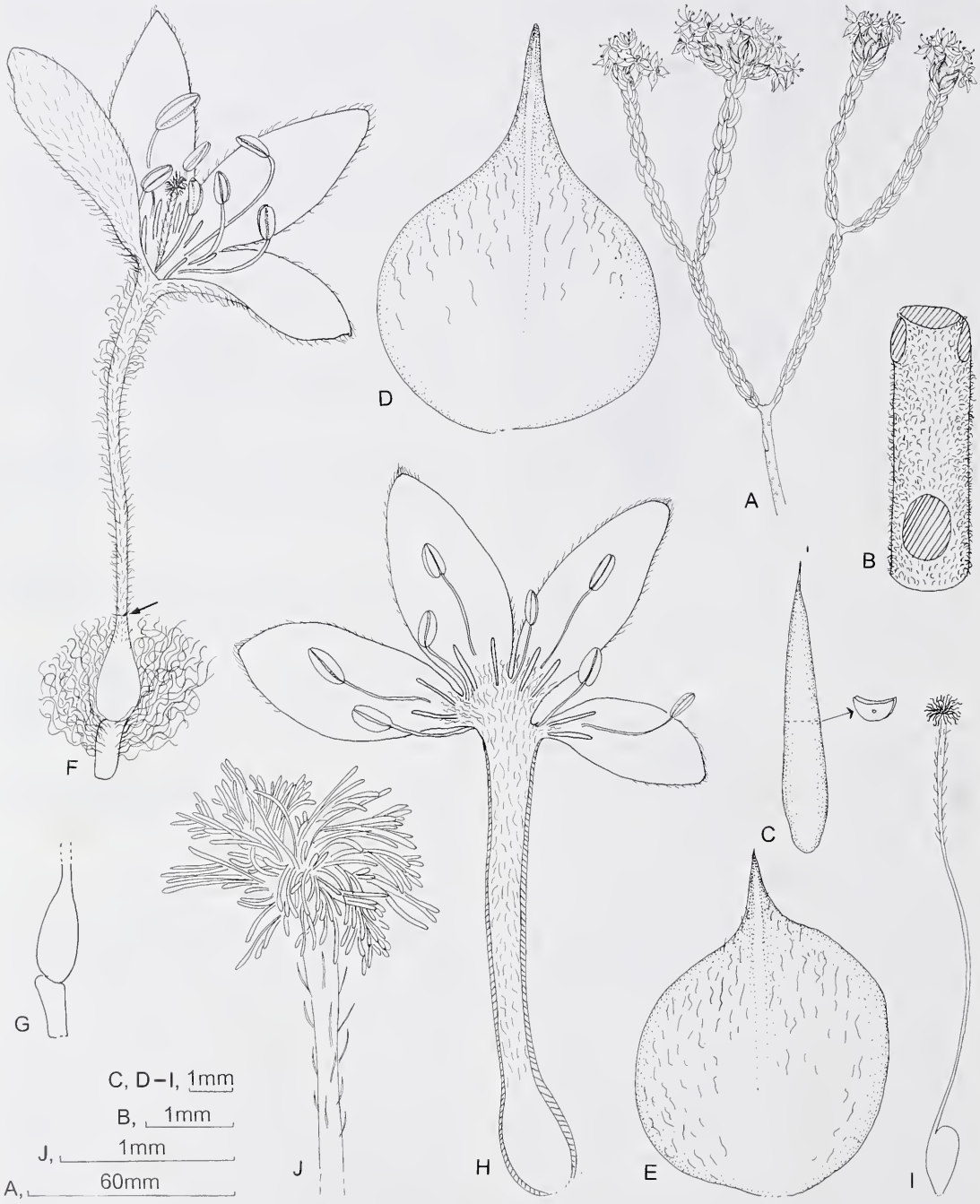

FIGURE 72.—*Lachnaea montana*. A, portion of plant; B, branch with leaves removed. C, D, leaf: C, abaxial view and c/s; D, bract-like leaf from pair subtending inflorescence. E, involucral bract. F, H, flower: F, circumscission zone arrowed; H, l/s with gynoecium removed. G, pedicel abaxially produced beyond point of attachment of flower (lateral view); I, gynoecium; J, stigma and upper portion of style. A, *Beyers 141* (NBG); B–J, *Beyers 267* (NBG). Scale bars: A, 60 mm; B–J, 1 mm.

stony soil at altitudes between 650 and 1 665 m (Figure 71). *Flowering time*: all months except June.

Conservation status: Lower Risk Least Concern (LRlc).

Diagnostic characters and relationships

Differs from the typical subspecies in resprouting after a fire and in having branches which are white-felted, at least when young. The two subspecies are allopatric.

Vouchers: *Beyers 246* (K, NBG, PRE); *Dahlgren & Peterson 1037* (K, NBG); *Hanekom 2723* (K, MO, NBG, NY, PRE, S); *Leipoldt 897* (BOL, NBG, PRE, SAM, Z); *Spreeth 142* (NBG, PRE); *Taylor 10601* (NBG, PRE). Total number of specimens examined: 142.

39. **Lachnaea montana** *Beyers*, sp. nov., primo adspectu *L. eriocephalae* similis, sed distincta inflorescentia bracteata, foliis bracteatis bracteisque involucratis eciliatis, sepalis plerumque plus minusve regularibus, sepalo anteriore ubi irregulari nunquam duplo amplitudine sepali posterioris, squamis linearibus in ore hypanthii pilis non tectis.

TYPE.—3218 (Clanwilliam): Piketberg Mountain, Farm Vergesig, northwest of homestead on west slope, 765 m, (–DC), 7-09-1997, *Beyers 267* (NBG, holo.!; BOL!, K!, MO!, PRE!, iso.).

Erect, moderately branched shrub up to 0.6 m tall, single-stemmed at base; reseeder. *Branches* ascending to inclined, semi-rigid, terete, internodes quarter to three-quarters as long as leaves, at first covered with short, crisped or straight hairs later glabrescent, leafy, becoming naked without prominent leaf scars. *Leaves* decussate, adpressed or ascending, scattered sessile, epistomatic, narrowly elliptic or lanceolate, 4.2–15.0 × 1.0–2.4 mm, coriaceous, glabrous; adaxially concave, enervate, ± white-punctulate, dull; abaxially convex, enervate or subkeeled towards apex, glossy; apex mucronate; base rounded; distal leaf pair subtending inflorescence bract-like, elliptic or obovate, 6.5–12.0 × 3.5–8.5 mm, coriaceous, green; adaxially concave, glabrous; abaxially convex, keeled, glabrous to tomentose abaxially; margin membranous, more so in upper half, yellow tinged maroon; apex mucronate or cuspidate; base cuneate. *Inflorescence* a terminal, sessile, bracteate, up to ± 40-flowered, capitulum-like umbel with up to 20 open flowers at a time, up to 30 mm diam., on main flowering branches or also on a few short lateral branches immediately below main inflorescence, forming a compact glomerule at apex of main flowering branch; bracteate umbel appears to be enclosed at base by 2 pairs of involucral bracts but only 1 pair immediately below flowers may be regarded as true bracts, as vegetative shoots develop in axils of subdistal pair. *Involucral bracts* 2, elliptic to widely ovate or obovate, 7.5–12.0 × 4–6 mm, coriaceous, green; adaxially concave, glabrous; abaxially convex, keeled, glabrous to tomentose abaxially; margin membranous, more so in upper half, yellow tinged maroon; apex mucronulate or cuspidate; base cuneate. *Flowers* ± actinomorphic, cream, mauve or dirty violet, pedicellate. *Pedicel* linear, abaxially produced beyond insertion of flower, 0.8–3.5 mm long, densely villous, elongating in fruiting stage. *Hypanthium* 7–17 mm long, circumscissile $^1/_5$–$^1/_3$ from base; upper portion narrowly funnel-shaped, sericeous or sericeous-hirsute outside, sericeous inside; basal portion narrowly ellipsoid to ovoid, outside puberulent in upper quarter, rest glabrous, glabrous inside. *Sepals* patent, ± equal to subequal, adaxially glabrous, abaxially sericeous, narrowly elliptic to elliptic, 3.5–8.0 × 1.5–4.0 mm, acute to rounded. *Stamens* exserted; outer, antesepalous whorl arising at base of sepals; inner, antepetalous whorl arising at rim of hypanthium, shorter than outer whorl; outer filaments 2.2–4.7 mm long, inner 1.2–3.1 mm long; anthers ellipsoid, 0.8–1.2 mm long, abaxially without broad connective tissue. *Floral scales* exserted, arising in mouth of hypanthium immediately below antepetalous stamens, linear, 0.4–2.1 mm long, glabrous, translucent in fresh state. *Ovary* narrowly ellipsoid to obovoid, 1.1–2.3 mm long, glabrous. *Style* linear, 5.5–16.0 mm long, sericeous in upper half to upper three-quarters, rest glabrous. *Stigma* brush-like (Figure 72).

Distribution and ecology

Lachnaea montana has a disjunct distribution. It is known from the Piketberg Mountain in the west, the Hex River Mountains south and southeast of Ceres and the Keeromsberg northeast of Worcester, at altitudes between 765 and 2 330 m. It grows in stony soils probably derived from shale (Figure 71). *Flowering time*: September to February.

Conservation status: Lower Risk Near Threatened (LRnt). The localized and scattered distribution of the populations puts the species at risk.

Diagnostic characters and relationships

Lachnaea montana superficially resembles *L. eriocephala*, but is easily recognized by its bracteate inflorescence, bract-like leaves and involucral bracts which are eciliate, by sepals which are usually more or less regular (when irregular, anterior sepal never twice the size of the posterior one), and by linear floral scales not obscured by hairs in the mouth of the hypanthium. It is allied to *L. globulifera*, from which it differs by the membranous, eciliate involucral bracts, narrowly elliptic to elliptic sepals and by linear floral scales which are not obscured by hairs in the mouth of the hypanthium. It is also closely related to *L. pedicellata*, from which it can be distinguished by the larger flowers and the linear, villous pedicels.

Vouchers: *Beyers 141* (K, MO, NBG, PRE); *Esterhuysen 8304* (BOL), *8421* (BOL); *Kotze 114* (NBG); *Marloth 2263* (PRE); *Winter 248* (NBG, PRE). Total number of specimens examined: 40.

40. **Lachnaea pedicellata** *Beyers*, sp. nov., *L. montanae* affinis sed ab ea differt floribus brevioribus, pedicellis dorsoventraliter complanatis et anguste obovatis ad obovatis apice plerumque emarginatis abaxialiter sericeis adaxialiter villosis.

TYPE.—3319 (Worcester): Ceres Dist., Waboomsberg, level area west of beacon, 1 770 m, (–AD), 24-11-1995, *Beyers 260* (NBG, holo.!; BOL!, K!, PRE!, iso.).

Passerina eriocephala Thunb., Prodromus plantarum capensium: 75 (1794); Thunb., Flora capensis: 375 (1823), non *Lachnaea eriocephala* L. Type: *Thunberg sheet 9575* [*Passerina eriocephala*] (UPS, lecto., here designated, –NBG, photo.!, –PRE, microfiche!; S! [*L. eriocephala* sub Herb. Montinii], S! [*L. eriocephala* sub Herb. Alstroemeri], isolecto.).

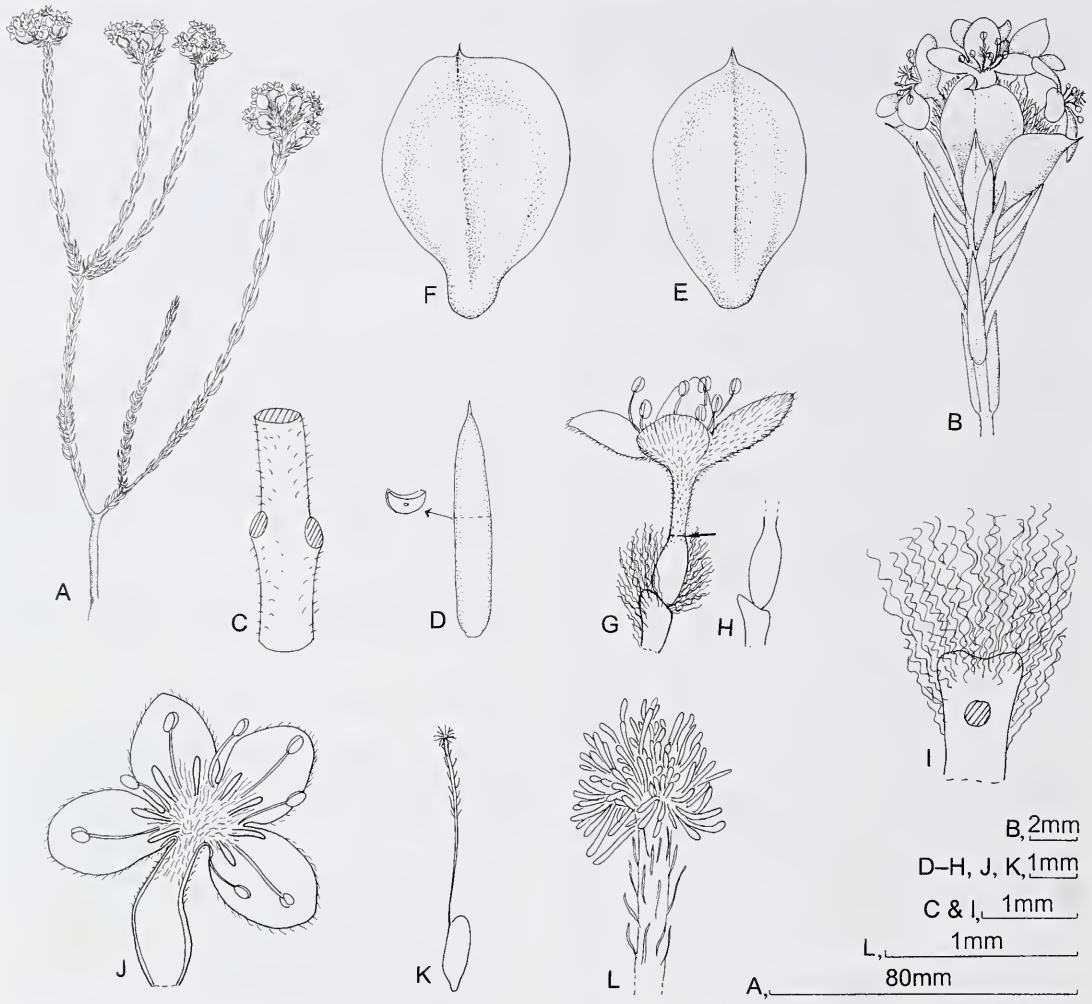

FIGURE 73.—*Lachnaea pedicellata*, *Beyers 260* (NBG). A, portion of plant; B, flowering branch; C, branch with leaves removed. D, E, leaf: D, abaxial view and c/s; E, bract-like leaf from pair subtending inflorescence. F, involucral bract. G, J, flower: G, circumscission zone arrowed; J, l/s with gynoecium removed. H, I, pedicel: H, abaxially produced beyond point of attachment of flower (lateral view); I, adaxial view. K, gynoecium; L, stigma and upper portion of style. Scale bars: A, 80 mm; B, 2 mm; C–L, 1 mm.

Erect, moderately branched shrub up to 0.6 m tall, single-stemmed at base, branching close to ground; reseeder. Branches ascending to inclined, slender, lax, terete, internodes $^1/_4$–$^3/_4$ as long as leaves, at first covered with short, crisped or straight hairs, later glabrescent, leafy, becoming naked without prominent leaf scars. *Leaves* decussate, adpressed to ascending, scattered, with those below inflorescence crowded, sessile, epistomatic, linear to narrowly elliptic, 4.5–12.0 × 0.8–1.5 mm, those below inflorescence gradually broader, ovate, up to 2.5 mm wide, coriaceous, glabrous; adaxially ± flat to concave, enervate, white-punctulate, dull; abaxially convex, enervate, glossy; apex mucronate; base rounded; distal leaf pair subtending inflorescence bract-like, obovate to widely obovate, 5.5–7.2 × 3.2–5.0 mm, coriaceous, glabrous, green; adaxially concave, glabrous; abaxially convex, keeled; margin membranous, more so in upper half, yellow usually tinged maroon; apex apiculate to cuspidate; base cuneate. *Inflorescence* a terminal, sessile, bracteate, ± 20-flowered, capitulum-like umbel with up to 8 open flowers at a time, up to 15 mm diam., on main flowering branches and also on a few short, lateral branches immediately below main inflorescence, forming a compact glomerule; bracteate umbel appears to be enclosed at base by 2 pairs of involucral bracts, but only 1 pair immediately below flowers may be regarded as being true bracts, as vegetative shoots develop in axils of subdistal pair. *Involucral bracts* 2, elliptic, or obovate to widely obovate occasionally emarginate, 6.0–7.5 × 3–7 mm, coriaceous, glabrous, green; adaxially concave; abaxially convex, keeled; margin membranous, more so in upper half, yellow usually tinged maroon; apex mucronulate or shortly cuspidate; base cuneate. *Flowers* ± actinomorphic, cream, pedicellate. *Pedicel* dorso-ventrally flattened, abaxially produced beyond point of attachment of flower, narrowly obovate to obovate in outline, 0.9–3.0 mm long,

elongating in fruiting stage, adaxially sericeous, abaxially villous, apex usually emarginate. *Hypanthium* 3.0–4.4 mm long, circumscissile $^1/_3$–$^1/_2$ from base; upper portion narrowly funnel-shaped, sericeous on both sides; basal portion ellipsoid, outside puberulent in upper quarter, rest glabrous, inside glabrous. *Sepals* patent, ± equal, adaxially glabrous, abaxially sericeous, elliptic to widely elliptic or widely ovate to very widely ovate, 2.1–3.8 × 1.6–2.6 mm, rounded to obtuse. *Stamens* exserted; outer, antesepalous whorl arising at base of sepals; inner, antepetalous whorl arising at rim of hypanthium, shorter than outer whorl; outer filaments 1.2–3.1 mm long, inner 0.7–2.5 mm long; anthers ellipsoid to widely ellipsoid, 0.4–0.8 mm long, abaxially without broad connective tissue. *Floral scales* exserted, arising at mouth of hypanthium immediately below antepetalous stamens, narrowly oblong or narrowly ellipsoid, 0.7–1.1 mm long, ± half to as long as antepetalous filaments, glabrous, pale yellow in fresh state. *Ovary* ellipsoid or obovoid 0.9–1.3 mm long, glabrous. *Style* linear or linear obconical, 3.0–4.3 mm long, sericeous in upper $^1/_3$–$^1/_2$, rest glabrous. *Stigma* brush-like (Figure 73).

Distribution and ecology

Lachnaea pedicellata has been recorded from the Cold Bokkeveld at altitudes between 1 760 and 1 830 m, growing in sandy loam soil probably on underlying shale (Figure 74). *Flowering time*: October to January.

Conservation status: Vulnerable (VU D2). Known from only a few collections most of which are old. It appears to be a localized species and being a reseeder, is vulnerable to frequent fires.

Diagnostic characters and relationships

Lachnaea pedicellata is allied to *L. montana* (no. 39), from which it is distinguished by the shorter flowers and the dorso-ventrally flattened pedicels which are narrowly obovate to obovate in outline with apex usually emarginate, sericeous abaxially, villous adaxially. The only other member of the genus with similar pedicels is *L. naviculifolia* (no. 36).

Etymology

The distinct pedicels in this species, shared only by one other species in the genus, prompted the specific epithet which is derived from the Latin word for pedicelled.

Vouchers: *Compton 12844* (NBG), *18719* (NBG); *Du Toit s.n.* (NBG, PRE); *Leighton 2219* (BOL); *Marloth 6252* (PRE); *Oliver 9282* (NBG). Total number of specimens examined: 13.

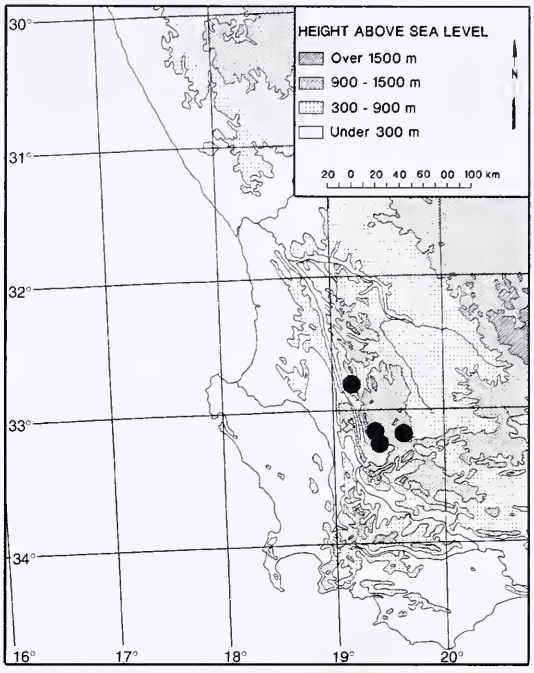

FIGURE 74.—Known distribution of *Lachnaea pedicellata*.

EXCLUDED SPECIES

Note: insufficiently known spp. and synonyms are in italics; names in roman type are accepted names.

Lachnaea ciliata (L.) Crantz: 129 (1766) = *Passerina ciliata* L.: 559 (1753). Description is inadequate and cited illustrations in the protologue are not *Lachnaea* species.

Lachnaea conglomerata L.: 560 (1753) = Phylica stipularis *L.* (*L. conglomerata* was proposed for rejection by Cafferty & Beyers 1999).

Lachnaea dodecandra (L.) Crantz: 129 (1766) = Struthiola dodecandra *(L.) Druce*: 425 (1914).

Lachnaea dubia Gand.: 417 (1913). Type: Cape, Table Mountain, *Debeaux s.n.* (LY, holo.!) identified as Gnidia laxa *(L.f.) Gilg*.

Lachnaea filiformis (L.) Crantz: 129 (1766) = Passerina filiformis *L.*: 559 (1753); C.H.Wright: 10 (1915).

Lachnaea hirsuta (L.) Crantz: 129 (1766) = Passerina hirsuta *L.*: 559. Description inadequate, however, according to the locality cited as, 'Hispania', it is not a *Lachnaea* species.

Lachnaea laevigata (L.) Crantz: 129 (1766) = *Passerina laevigata* L.: 513 (1762 = Gnidia oppositifolia *L.*; C.H.Wright: 47 (1915).

Lachnaea sericea (L.) Crantz: 129 (1766) = *Passerina sericea* L.: 513 (1762) = Gnidia sericea *(L.) L.*; C.H.Wright: 63 (1915).

Lachnaea sphaerocephala Burm.f.:12 (1768). The brief description mentions adpressed, twisted leaves, a condition not found in any of the *Lachnaea* species.

Cryptadenia ciliata (Thunb.) Meisn.: 407 (1840) = *Passerina ciliata* Thunb.: 75 (1794) non L.: 559 (1753) = Gnidia penicillata *Licht. ex Meisn.*; Peterson: 476 (1959).

8. Conclusions

Taxonomy

Lachnaea is endemic to the Cape Floristic Region (CFR). Currently it comprises 40 species and two subspecies. The circumscription of *Lachnaea* has been extended to include the genus *Cryptadenia* (previously with five species).

Two cladistic analyses, one with *Struthiola leptantha* as the outgroup (Analysis A) and another with multiple taxa as the outgroup (Analysis B) were done. The cladistic analysis showed that the sections *Sphaeroclinium*, *Conoclinium* and *Microclinium*, established by Meisner (1840), are paraphyletic and are therefore not upheld. No other sections are maintained; the resolution of such species groups is not clear. Analyses A and B produced conflicting results with regard to the hypothetical evolutionary pathway of certain characters. All available evidence, however, strongly supports the monophyletic status of the genus. The hypothesis of relationships within *Lachnaea* presented here should be seen as a starting point and by no means as the final word.

Allopatric speciation appears to have been the most important speciation mechanism in *Lachnaea*. Additional variables, along which diversification may have taken place, are altitudinal difference, allochrony and regeneration strategy of species after fire.

Lachnaea is easily distinguished from other genera of the Thymelaeaceae in southern Africa by the eight floral scales, which arise on the upper portion of the hypanthium below the insertion of the two stamen whorls.

Morphology

The following characters proved to be of particular taxonomic significance:

- regeneration strategy (reseeder vs resprouter)
- leaf characters, for example phyllotaxis, indumentum of leaf margins, absence or presence of parallel ribs on abaxial leaf surface
- type of inflorescence
- floral characters: pedicel—present or absent, point of attachment of flower, whether elongating in fruiting stage; hypanthium—shape, indumentum and trichome shape; sepals—zygomorphy, colour and indumentum; androecium—position of insertion and whether exserted or enclosed; anther with or without broad connective tissue abaxially; floral scales—position of insertion on hypanthium, whether exserted or enclosed, whether basally or abaxially attached to hypanthium wall, shape and indumentum; stigma—shape and length of papillae

Anatomy

Taxonomically the most useful leaf anatomical characters include: whether the leaves are amphi- or epistomatic; stomata sunken or on same level as adjacent epidermal cells; presence of prominent extraxylary fibres capping mid- and lateral vascular bundles; presence of extraxylary fibres not associated with the vascular bundles, running parallel to the leaf margins in the mesophyll; presence of diosmin crystals.

Anatomical adaptations in the leaves of *Lachnaea* are considered to be typical of plants able to withstand the long, dry summers of the mediterranean or semi-mediterranean climate of the CFR.

Palynology

Palynology is unimportant in the delimitation of the genera in the subtribe Gnidiinae and in the delimitation of the species in *Lachnaea*. All these groups are characterized by pollen grains which are spheroid in shape, pantoporate, and with a *Croton*-pattern. The surface structure of the triangular supratectal subunits revealed a continuum of variation.

Chromosome number

Chromosome number is taxonomically insignificant at the generic and specific level. All the members of the genus investigated have 2n = 18.

Phytogeography

Members of *Lachnaea* occur almost exclusively in fynbos vegetation on oligotrophic soils derived from the orthoquartzites of the Cape Supergroup. A few species occur on shale or limestone. Most species can be regarded as montane. The centre of diversity for *Lachnaea* species falls in the 3319 (Worcester) degree grid with the main concentration of species in the quarter degrees 3319 AD and AA (Figure 11). *Lachnaea* demonstrates a high percentage of regional endemism with 55% of the species endemic to the Northwestern, Southwestern, Karoo Mountain and Langeberg Centres of the CFR. Although species of *Lachnaea* also occur in the Bredasdorp-Riversdale and Southeastern Centres, none of the species are endemic there.

Conservation

Many of the species appear to be relictual and particularly vulnerable to disturbance and to too frequent burning. The conservation status of each species was evaluated and the IUCN Red List Categories (Walter & Gillett 1998) were assigned as follows: 18 species—Vulnerable; 18 species—Lower Risk Least Concern; two species—Lower Risk Near Threatened; one species—Extinct; and one species—Data Deficient.

9. References

AITON, W.T. 1811. *Hortus Kewensis; or, a catalogue of the plants cultivated in the Royal Botanic Garden at Kew*. edn 2, vol. 2. Longman, London.

ANDREWS, H.C. 1800. *Lachnaea eriocephala*. *The botanist's repository* 2: t. 104. London.

ANDREWS, H.C. 1803. *Lachnaea purpurea*. *The botanist's repository* 5: t. 293. London.

ANDREWS, H.C. 1808. *Laclnaea buxifolia*. *The botanist's repository* 8: t. 524. London.

ANGIOSPERM PHYLOGENY GROUP (APG). 1998. An ordinal classification for families of flowering plants. *Annals of the Missouri Botanical Garden* 85: 531–553.

ARNOLD, T.H. & DE WET, B.C. 1993. Plants of southern Africa: names and distribution. *Memoirs of the Botanical Survey of South Africa* No. 62: 1–825.

BAILLON, H. 1880. *The natural history of plants* 6. Reeve, London.

BARTHLOTT, W., NEINHUIS, C., CUTLER, D., DITSCH, F., MEUSEL, I., THEISEN, I. & WILHELMI, H. 1998. Classification and terminology of plant epicuticular waxes. *Botanical Journal of the Linnean Society* 126: 237–260.

BATTEN, A & BOKELMANN, H. 1966. *Wild flowers of the Eastern Cape Province*. Books of Africa, Cape Town.

BENTHAM, G. & HOOKER, J.D. 1880. *Genera plantarum* 3. Reeve, London.

BERGIUS, P.J. 1767. *Descriptiones plantarum ex Capite Bonae Spei*. Salvius, Stockholm.

BEYERS, J.B.P. 1992. *The generic delimitation of* Lachnaea *and* Cryptadenia *(Thymelaeaceae)*. M.Sc. thesis, University of Stellenbosch, Stellenbosch. Unpublished.

BEYERS, J.B.P. 1997. New combinations in *Lachnaea*. *Bothalia* 27: 45.

BEYERS, J.B.P. & MARAIS, E.M. 1998. Palynological studies of the Thymelaeaceae of the Cape Flora. *Grana* 37: 193–202.

BEYERS, J.B.P. & VAN DER WALT, J.J.A. 1994. Inflorescence morphology of *Lachnaea* and *Cryptadenia* (Thymelaeaceae). *Bothalia* 24: 195–202.

BEYERS, J.B.P. & VAN DER WALT, J.J.A. 1995. The generic delimitation of *Laclnaea* and *Cryptadenia* (Thymelaeaceae). *Bothalia* 25: 65–85.

BEYERS, J.B.P. & VAN WYK, A.E. 1998a. A new species of *Lachnaea* (Thymelaeaceae) from the Western Cape. *South African Journal of Botany* 64: 66–69.

BEYERS, J.B.P. & VAN WYK, A.E. 1998b. A new species of *Lachnaea* endemic to the southeastern mountains of the Western Cape (Thymelaeaceae). *Bothalia* 28: 49–53.

BHAT, B.K., BAKSHI, S.K. & KAUL, M.K. 1974. In A. Löve, IOPB chromosome number reports XLIII. *Taxon* 23: 193–196.

BJORKQVIST, I., VON BOTHMER, R., NILSSON, O. & NORDENSTAM, B. 1969. Chromosome numbers in Iberian Angiosperms. *Botaniska Notiser* 122: 271–283.

BOND, P. 1982. A new combination in *Lachnaea* L. (Thymelaeaceae). *Journal of South African Botany* 48: 527.

BOND, P. & GOLDBLATT, P. 1984. Plants of the Cape Flora. A descriptive catalogue. *Journal of South African Botany*, Suppl. vol. 13: 1–455.

BREDENKAMP, C.L. & BEYERS, J.B.P. 2000. Thymelaeaceae. In O.A. Leistner, Seed plants of southern Africa: families and genera. *Strelitzia* 10: 544–546. National Botanical Institute, Pretoria.

BREDENKAMP, C.L. & VAN WYK, A.E. 1996. Palynology of the genus *Passerina* (Thymelaeaceae): relationships, form and function. *Grana* 35: 335–346.

BREDENKAMP, C.L. & VAN WYK, A.E. 1999. Structure of mucilaginous epidermal cell walls in *Passerina* (Thymelaeaceae). *Botanical Journal of the Linnean Society* 129: 223–238.

BREMER, K. 1976. The genus *Relhania* (Compositae). *Opera Botanica* 40: 1–85.

BROWN, N.E. 1901. *L. passerinoides*. *Kew Bulletin* 1901: 132.

BRUMMITT, R.K. 1992. *Vascular plant families and genera*. Royal Botanic Gardens, Kew.

BRUMMITT, R.K. & POWELL, C.E. 1992. *Authors of plant names*. Royal Botanic Gardens, Kew.

BUNNINGER, L. 1972. Untersuchungen über die morphologische Natur des Hypanthiums bei Myrtales und Thymelaeales-Familien. II. Myrtaceae. III. Vergleich mit den Thymelaeaceae. *Beiträge zur Biologie der Pflanzen* 48: 79–156.

BURMAN, J. 1737. *Thesaurus zeylanicus*. Janssonius-Waesberg & Salomon Schouten, Amsterdam.

BURMAN, J. 1739. *Rariorum africanarum plantarum*, Dec. 5. Boussière, Amsterdam.

BURMAN, N.L. 1768. *Flora indica*. Haak, Leiden; Schreuder, Amsterdam.

CAFFERTY, S. & BEYERS, J. 1999. (1398) Proposal to reject the name *Lachnaea conglomerata* (Rhamnaceae). *Taxon* 48: 171, 172.

CARLQUIST, S. 1990. Leaf anatomy of Geissolomataceae and Myrothamnaceae as a possible indicator of relationship to Bruniaceae. *Bulletin of the Torrey Botanical Club* 117: 420–428.

CARNOY, J.B. 1886. La cytodierèse de l'oeuf. *Cellule* 3: 1–92.

CLASSEN-BOCKHOFF, R. 1990. Pattern analysis in pseudanthia. *Plant Systematics and Evolution* 171: 57–88.

COMPTON, R.H. 1934a. *Lachnaea elegans*. *Journal of Botany, British and Foreign* 72: 20, 21.

COMPTON, R.H. 1934b. *Lachnaea naviculaefolia*. *Journal of Botany, British and Foreign* 72: 21.

COMPTON, R.H. 1953. *Lachnaea ruscifolia*. *Journal of South African Botany* 19: 132–134.

COWLING, R.M. 1992. *The ecology of fynbos: nutrients, fire and diversity*. Oxford University Press, Cape Town.

CRANTZ, H.J.N. 1766. *Institutiones rei herbariae* 1. Kraus, Wien.

CRONQUIST, A. 1978. Once again, what is a species? In Biosystematics in agriculture. *Beltsville Symposia in Agricultural Research* 2: 3–20.

CRONQUIST, A. 1981. *An integrated system of classification of flowering plants*. Columbia University Press, New York.

CURTIS, W. 1795. *Passerina grandiflora*. *The Botanical Magazine* 9: t. 292. London.

CUTTER, E.G. 1978. *Plant anatomy. Part 1: cells and tissues*, edn 2. Clowes, London.

DAHLGREN, R. 1963. Studies on *Aspalathus*. Phytogeographical aspects. *Botaniska Notiser* 116: 431–472.

DAHLGREN, R. 1969. Distribution and substrate in the South African genus *Aspalathus* L. (Leguminosae). *Botaniska Notiser* 128: 505–534.

DAHLGREN, R. 1971. Current topics. Multiple similarity of leaf between two genera of Cape plants, *Cliffortia* L. (Rosaceae) and *Aspalatlus* L. (Fabaceae). *Botaniska Notiser* 124: 292–304.

DAHLGREN, R. 1975. A system of classification of the angiosperms to be used to demonstrate the distribution of characters. *Botaniska Notiser* 128: 119–147.

DAHLGREN R. & THORNE, R.F. 1984. The order Myrtales: circumscription, variation, and relationships. *Annals of the Missouri Botanical Garden* 71: 633–699.

DE JUSSIEU, A.L. 1789. *Genera plantarum*. Herissant & Barrois, Paris.
DOMKE, W. 1934. Untersuchungen über die systematische und geographische Gliederung der Thymelaeaceen nebst einer Neubeschreibung ihrer Gattungen. *Bibliotheca Botanica* 27: 1–151.
DRÈGE, J.F. 1843. *Zwei pflanzengeografische Dokumente nebst einer Einleitung von E. Meyer*. Besondere Beigabe zur *Flora* 1843, Band II.
DRÈGE, J.F. 1847a. Standörterverzeichniss der von C.L. Zeyher in Südafrika gesammelten Pflanzen. *Linnaea* 19: 583–598.
DRÈGE, J.F. 1847b. Vergleichungen der von Ecklon und Zeyher und von Drège gesammelten südafrikanischen Pflanzen (so weit dieselben noch vorhanden) mit den Exemplaren von Zeyher's neuesten Sammlungen, welche derselbe zum Verkauf stellt durch J.F. Drège in Borstel bei Hamburg. *Linnaea* 20: 183–258.
DRUCE, G.C. 1914. Notes on nomenclature. *Report. Botanical Exchange Club of the British Isles* 1913: 405–425.
DYER, R.A. 1975. *The genera of southern African flowering plants*, Vol. 1. Department of Agricultural Technical Services, Pretoria.
EDWARDS, D. & LEISTNER, O.A. 1971. A degree reference system for citing biological records in southern Africa. *Mitteilungen der Botanischen Staatssammlung, München* 10: 501–509.
EICHLER, A.W. 1878. *Blüthendiagramme*, vol. 2. Engelmann, Leipzig.
ENDLICHER, S. 1836–1840. *Genera plantarum*. Beck, Vienna.
ERDTMAN, G. 1966. *Pollen morphology and plant taxonomy. Angiosperms*. Almqvist & Wiksell, Stockholm.
ESAU, K. 1965. *Plant anatomy*, edn 2. Wiley, New York.
FAHN, A. 1990. *Plant anatomy*, edn 4. Pergamon Press, Oxford.
FARRIS, J. S. 1969. A successive weighting approach to character weighting. *Systematic Zoology* 18: 374–385.
FARRIS, J.S. 1988. *Hennig86 version1.5. Program and software documentation*. Port Jefferson Station, New York.
FOURCADE, H.G. 1934. Contributions to the flora of the Knysna and neighbouring divisions. *Transactions of the Royal Society of South Africa* 21: 75–102.
GAERTNER, C.F. 1807. *Supplementum carpologicae*, fascicle 2, part 2. Richter, Leipzig.
GANDOGER, M. 1913. L'herbier africain de Sonder. *Bulletin de la Société Botanique de France* 60: 414–422.
GIBSON, A.C. 1998. Photosynthetic organs of desert plants—structural designs of nonsucculent desert plants cast doubt on the popular view that saving water is the key strategy. *BioScience* 48: 911–920.
GILG, E. 1894. Thymelaeaceae. In A. Engler & K. Prantl, *Die natürlichen Pflanzenfamilien* III, 6a: 216–245. Engelmann, Leipzig.
GOLDBLATT, P. 1978. An analysis of the flora of southern Africa: its characteristics, relationships and origins. *Annals of the Missouri Botanical Garden* 65: 369–436.
GOLDBLATT, P. 1981. Systematics and biology of *Homeria* (Iridaceae). *Annals of the Missouri Botanical Garden* 68: 413–503.
GOLDBLATT, P. & MANNING, J. 2000. Cape plants. A conspectus of the Cape Flora of South Africa. *Strelitzia* 9. National Botanical Institute, Pretoria.
GOOD, R. 1974. *The geography of the flowering plants*, edn 4. Longman, London.
GRANT, V. 1981. *Plant speciation*, edn 2. Columbia University Press, New York.
GUNN, M. & CODD, L.E. 1981. *Botanical exploration of South Africa*. Balkema, Cape Town.
GUPTA, S. & GILLETT, G.W. 1969. Observations on Hawaiian species of *Wikstroemia* (Angiospermae: Thymelaeaceae). *Pacific Science* 23: 83–88.
HABERLANDT, G. 1914. *Physiological plant anatomy*. Reprint edn 1965. Today & Tomorrow's Book Agency, New Delhi.
HARON, N.W. & MOORE, D.M. 1996. The taxonomic significance of leaf micromorphology in the genus *Eugenia* L. (Myrtaceae). *Botanical Journal of the Linnean Society* 120: 265–277.
HAUSER, D.L. & PRESCH, W. 1991. The effect of ordered characters on phylogenetic reconstruction. *Cladistics* 7: 243–265.
HEADS, M.J. 1990. A revision of the genera *Kelleria* and *Drapetes* (Thymelaeaceae). *Australian Systematic Botany* 3: 595–652.
HEINIG, K.M. 1951. Studies in the floral morphology of the Thymelaeaceae. *American Journal of Botany* 38: 113–132.
HEYWOOD, V.H. 1979. *Flowering plants of the world*. Oxford University Press, Oxford.
HOLMGREN, P.K., HOLMGREN, N.H. & BARNETT, L.C. 1990. Index Herbariorum 1. The herbaria of the world, edn 8. *Regnum Vegetabile* 120: 1–693.
HOOKER, W.J. 1845. *Cryptadenia uniflora*. *Curtis's Botanical Magazine* 71: t. 4143.
HUTCHINSON, J. 1959. *The families of flowering plants*, vol. 1. Dicotyledons, edn 2. Clarendon Press, London.
HUTCHINSON, J. 1969. *Evolution and phylogeny of flowering plants*. Academic Press, London.
JACKSON, B.P. & SNOWDON, D.W. 1990. *Atlas of microscopy of medicinal plants, culinary herbs and spices*. Belhaven Press, London.
JOEL, D.M. 1983. A.G.S. (Alcian Green Safranin)—a simple differential staining of plant material for light microscopy. *Proceedings Royal Microscopical Society* 18: 149.
JOHANSEN, D.A. 1940. *Plant microtechnique*. McGraw-Hill, New York.
JORDAAN, A. & THEUNISSEN, J.D. 1992. Phenolic deposits and tannin in the leaves of five xerophytic species from southern Africa. *Botanical Bulletin of Academia Sinica* 33: 55–61.
KARIS, P.O. 1989. Systematics of the genus *Metalasia* (Asteraceae-Gnaphalieae). *Opera Botanica* 99: 1–150.
KEARNS, C.A. & INOUYE, D.W. 1993. *Techniques for pollination biologists*. University Press of Colorado, Colorado.
KEATING, R.C. 1984. Leaf histology and its contribution to relationships in the Myrtales. *Annals of the Missouri Botanical Garden* 71: 801–803.
KUNZE, H. 1990. Morphology and evolution of the corona in Asclepiadaceae and related families. *Tropische und subtropische Pflanzenwelt* 76: 1–51.
KUZMANOV, B. 1973. In A. Löve, IOPB chromosome number reports XLII. *Taxon* 22: 647–654.
LAMARCK, J.B.A.P.M. DE 1792. Encyclopédie méthodique. *Dictionnaire encyclopédique de botanique* 3. Panckoucke, Paris.
LEVYNS, M.R. 1950. Thymelaeaceae. In R.S. Adamson & T.N. Salter, *Flora of the Cape Peninsula*. Juta, Cape Town.
LINDER, H.P. 1985. Gene flow, speciation, and species diversity patterns in a species-rich flora: the Cape flora. In E.S. Vrba, Species and speciation: 53–57. *Transvaal Museum Monograph* 4. Transvaal Museum, Pretoria.
LINNAEUS, C. 1740. *Systema naturae*, edn 2. Kiesewetter, Stockholm.
LINNAEUS, C. 1742. *Genera plantarum*, edn 2. Wishoff, Leiden.
LINNAEUS, C. 1753. *Species plantarum*, edn 1. Salvius, Stockholm.
LINNAEUS, C. 1754. *Genera plantarum*, edn 5. Salvius, Stockholm.
LINNAEUS, C. 1762. *Species plantarum*, edn 2. Salvius, Stockholm.
LINNAEUS, C. 1764. *Amoenitates academicae* 6. Wetstenius, Lugduni Batavorum.
LINNAEUS, C. fil. 1782. *Supplementum plantarum*. Orphanotropheus, Braunschweig.
LODDIGES, C. 1818. *The botanical cabinet*. John & Arthur Arch, London.
LOEVE, A. & KJELLQVIST, E. 1974. Cytotaxonomy of Spanish plants IV. Dicotyledons: Caesalpiniaceae–Asteraceae. *Lagascalia* 4: 153–211.
LOISELEUR-DESLONGCHAMPS, J.L.A. 1820. *Herbier général de l'amateur* 4: t. 234. Paris.
LUCKOW, M. 1995. Species concepts: assumptions, methods and applications. *Systematic Botany* 20: 589–605.
LUNDGREN, J. 1972. Revision of the genus *Anaxeton* Gaertn. (Compositae). *Opera Botanica* 31: 1–59.
LYSHEDE, O.B. 1977. Studies on the mucilaginous cells in the leaf of *Spartocytisus filipes* W.B. *Planta* 133: 255–260.
MABBERLEY, D.J. 1997. *The plant-book*, edn 2. Cambridge University Press, Cambridge.
MAJOVSKY, J. ET AL. 1974. Index of chromosome numbers of Slovkian flora, part 4. *Acta Facultatis Rerum Naturalium Universitatis Comenianae, Botanica* 23: 1–23.
MASON, H. 1972. *Western Cape sandveld flowers*. Struik, Cape Town.
MATHEW, P.M. & VALSALADEVI, G. 1989. Pollen dimorphism in the Indian Acanthaceae. *Journal of Palynology* 25: 107–111.
MATTATIA, J. 1965. *Floral morphology and vascular anatomy of some species of* Struthiola. B.Sc. Hons. thesis, University of Cape Town, Rondebosch. Unpublished.

MAYER, S.S. 1991. Morphological variation in Hawaiian *Wickstroemia* (Thymelaeaceae). *Systematic Botany* 16: 693–704.
MCDADE, L.A. 1995. Species concepts and problems in practice: insights from botanical monographs. *Systematic Botany* 20: 606–622.
MCDONALD, D.J. 1993. The vegetation of the southern Langeberg, Cape Province. 1. The plant communities of the Boosmansbos Wilderness Area. *Bothalia* 23: 129–151.
MEISNER, C.F. 1840. Synopsis Thymelaearum, Polygonearum et Begoniarum Africae Australis, imprimus a cl. J.J. Drège lectarum. *Linnaea* 14: 385–516.
MEISNER, C.F. 1843. Contributions towards a Flora of South Africa. *London Journal of Botany* 2: 527–559.
MEISNER, C.F. 1857. Thymelaeaceae. In A.P. de Candolle, *Prodromus systematis naturalis regni vegetabilis* 14: 573–580. Victoris Masson, Paris.
MELCHIOR, H. 1964. Myrtiflorae. In H. Melchior, *A. Engler's Syllabus der Pflanzenfamilien*. 12 Aufl., Bd. 2. Gebrüder Bornträger, Berlin-Nikolassee.
METCALFE, C.R. & CHALK, L. 1950. *Anatomy of the dicotyledons*, 2 vols. Clarendon Press, Oxford.
METCALFE, C.R. & CHALK, L. 1979. *Anatomy of the dicotyledons*, edn 2, vol. 1. Clarendon Press, Oxford.
METCALFE, C.R. & CHALK, L. 1983. *Anatomy of the dicotyledons*, edn 2, vol. 2. Clarendon Press, Oxford.
MULLER, J. 1979. Form and function in Angiosperm pollen. *Annals of the Missouri Botanical Garden* 66: 593–632.
NANDI, O.I., CHASE, M.W. & ENDRESS, P.K. 1998. A combined cladistic analysis of angiosperms using *rbc*L and non-molecular data sets. *Annals of the Missouri Botanical Garden* 85: 137–212.
NEVLING, L.I. & WOODBURY, R. 1966. Rediscovery of *Daphnopsis helleriana*. *Journal of the Arnold Arboretum* 47: 262–265.
NIXON, K. 1993. *CLADOS, Version 1.2. Program and documentation*. Trumansburg, New York.
NIXON, K.C. & CARPENTER, J. M. 1993. On outgroups. *Cladistics* 9: 413–426.
NORDENSTAM, B. 1969. Phytogeography of the genus *Enryops* (Compositae). Contribution to the phytogeography of southern Africa. *Opera Botanica* 23: 1–77.
NOWICKE, J.W. 1994. A palynological study of Crotonoideae (Euphorbiaceae). *Annals of the Missouri Botanical Garden.* 81: 245–269.
NOWICKE, J.W., PATEL, V. & SKVARLA, J.J. 1985. Pollen morphology and the relationships of *Aëtoxylon*, *Amyxa*, and *Gonystylus* to the Thymelaeaceae. *American Journal of Botany* 72: 1106–1113.
OLIVER, E.G.H., LINDER, H.P. & ROURKE, J.P. 1983. Geographical distribution of present-day Cape taxa and their phytogeographical significance. *Bothalia* 14: 427–440.
PETERSON, B. 1959. Some interesting species of *Gnidia*. *Botaniska Notiser* 112: 465–480.
POIRET, J.L.M. 1804. Encyclopédie méthodique. In J.B.A.P.M. de Lamarck, *Dictionnaire encyclopédique de botanique* 5. Paris.
POZHIDAEV, A.E. 1993. Polymorphism of pollen in the genus *Acer* (Aceraceae). *Grana* 32: 79–85.
PUNT, W., BLACKMORE, S., NILSSON, S & LE THOMAS, A. 1994. *Glossary of pollen and spore terminology*. LPP Contributions series No. 1, LPP Foundation, Utrecht.
RADFORD, A.E., DICKISON, W.C., MASSEY, J.R. & BELL, C.R. 1974. *Vascular plant systematics*. Harper & Row, New York.
RAO, V.S. & DAHLGREN, R. 1969. The floral anatomy and relationships of Oliniaceae. *Botaniska Notiser* 122: 161–171.
RENDLE, A. B. 1938. *The classification of flowering plants*, II. Cambridge University Press, Cambridge.
ROURKE, J.P. 1972. Taxonomic studies on *Lencospermum* R.Br. *Journal of South African Botany*, Suppl. vol. 8: 1–194.
SALISBURY, R.A. 1808. *Lachnaea glauca*. In W. Hooker, *Paradisus londinensis* 2. Hooker, London.
SAUNDERS, E.R. 1939. *Floral morphology*, II. Heffer, Cambridge.
SCHINZ, H. 1895. *Lachnaea funicanlis*. *Bulletin de l'Herbier Boissier* 3: 408 (112).
SCHLECHTER, F.R.R. 1896. Decades plantarum novarum Austro-Africanarum. *Journal of Botany, British and Foreign, London* 34: 500–504.
SCHLECHTER, F.R.R. 1898. Plantae Schlechterianae novae vel minus cognitae describuntur I. *Botanische Jahrbücher* 24: 434–459.
SHARMA, A. & SARKAR, A.K. (eds). 1967–1968. Chromosome number reports of plants in Annual Report, Cytogenetics Laboratory, Department of Botany, University of Calcutta. *The Research Bulletin* 2: 38–48.
SIMS, J. 1810. *Lachnaea eriocephala*. *Curtis's Botanical Magazine* 32: t. 1295.
SIMS, J. 1813. *Lachnaea purpurea*. *Curtis's Botanical Magazine* 39: t. 1594.
SIMS, J. 1814a. *Lachnaea buxifolia (α) virens*. *Curtis's Botanical Magazine* 39: t. 1657.
SIMS, J. 1814b. *Lachnaea buxifolia (β) glauca*. *Curtis's Botanical Magazine* 39: t. 1658.
SNOW, R. 1963. Alcoholic hydrochloric acid-carmine as a stain for chromosomes in squash preparations. *Stain Technology* 38: 9–13.
SOLEREDER, H. 1908. *Systematic anatomy of the dicotyledons*, vol. 2. Clarendon Press, Oxford.
SPRENGEL, K. 1825. *Systema vegetabilium*, vol 2. Libraria Dieterichiana, Göttingen.
STACE, C.A. 1989. *Plant taxonomy and biosystematics*, edn 2. Edward Arnold, London.
STAFLEU, F.A. & COWAN, R.S. 1976–1988. *Taxonomic literature*, edn 2. Bohn, Scheltema & Holkema, Utrecht.
STEARN, W.T. 1973. *Botanical Latin*, edn 2. David & Charles, Newton Abbot.
STEVENS, P.F. 1991. Character states, morphological variation, and phylogenetic analysis: a review. *Systematic Botany* 16: 553–583.
STRID, A.K. 1972. Revision of the genus *Adenandra* (Rutaceae). *Opera Botanica* 32: 1–112.
SWOFFORD, D.L. 1993. PAUP: *Phylogenetic Analysis using Parsimony*, Version 3.1.1. Illinois Natural History Survey, Champaign.
TAKHTAJAN, A.L. 1969. *Flowering plants: origin and dispersal*, English edn. Oliver & Boyd, Edinburgh.
TAKHTAJAN, A.L. 1986. *Floristic regions of the world*, English edn. University of California Press, Berkeley.
TAKHTAJAN, A.L. 1997. *Diversity and classification of flowering plants*. Columbia University Press, New York.
TAYLOR, H.C. 1980. Phytogeography of fynbos. *Bothalia* 13: 231–235.
THIELE, K. 1993. The holy grail of the perfect character: the cladistic treatment of morphometric data. *Cladistics* 9: 275–340.
THODAY, D. 1921. On the behaviour during drought of leaves of two Cape species of *Passerina*, with some notes on their anatomy. *Annals of Botany* 35: 585–601.
THODAY, D. 1924. A revision of *Passerina*. *Kew Bulletin* 1924: 146–168.
THORNE, R.F. 1968. Synopsis of a putatively phylogenetic classification of the flowering plants. *Aliso* 6: 57–66.
THORNE, R.F. 1976. A phylogenetic classification of the Angiospermae. *Evolutionary Biology* 9: 35–106.
THORNE, R.F. 1981. Phytochemistry and angiosperm phylogeny: a summary statement. In D.A. Young & D.S. Seigler, *Phytochemistry and angiosperm phylogeny*. Praeger, New York.
THUNBERG, C.P. 1794. *Prodomus plantarum capensium*, part 1. Edman, Uppsala.
THUNBERG, C.P. 1823. *Flora capensis*, edn J.A. Schultes. Cotta, Stuttgart.
TURCZANINOW, N.S. 1852. Decas septima generum adhuc non descriptorum adjectis descriptionibus nonnullarum specierum. *Bulletin de la Société Impériale des Naturalistes de Moscou* 25:138–181.
TURCZANINOW, N.S. 1853. Beiträge zur systematischen Botanik. VIII. Decas septima generum adhuc non descriptorum adjectis descriptionibus nonnullarum specierum. *Flora* 36: 729–744.
VAN DER MERWE, A.M. 1992. *A study to determine anatomical and morphological adaptations in the leaves of selected fynbos species*. M.Sc. thesis, University of Stellenbosch, Stellenbosch. Unpublished.
VAN DER MERWE, A.M., VAN DER WALT, J.J.A. & MARAIS, E.M. 1994. Anatomical adaptions in the leaves of selected fynbos species. *South African Journal of Botany* 60: 99–107.
VAN DER WALT, J.J.A. & VORSTER, P.J. 1983. Phytogeography of *Pelargonium*. *Bothalia* 14: 517–523.
VAN WYK, C.M. 1993. Thymelaeaceae. In T.H. Arnold & B.C. de Wet, Plants of southern Africa: names and distribution. *Memoirs of the Botanical Survey of South Africa* No. 62: 515–519.

WALTER, K.S. & GILLETT, H.J. 1998. *1997 IUCN Red List of Threatened Plants*. Compiled by the World Conservation Monitoring Centre. IUCN—The World Conservation Union, Switzerland & Cambridge, UK.

WEBERLING, F. 1983. Fundamental features of modern inflorescence morphology. *Bothalia* 14: 917–922.

WEBERLING, F. & HERKOMMER, U. 1989. Untersuchungen zur Infloreszenz-Morphologie der Thymelaeaceen. *Tropische und subtropische Pflanzenwelt* 68: 1–124.

WEIMARCK, H. 1941. Phytogeographical groups, centres and intervals within the Cape Flora. *Lunds Universitets Årsskrift*, Avd. 2, 37: 1–143.

WENDLAND, J.C. 1798. *Botanische Beobachtungen nebst einigen neuen Gattungen und Arten*. Hahn Brothers, Hannover.

WENT, F.W. 1971. Parallel evolution. *Taxon* 20: 197–226.

WETTSTEIN, R. 1935. *Handbuch der systematischen Botanik*. Deuticke, Leipzig & Wien.

WIENS, J.J. 1995. Polymorphic characters in phylogenetic systematics. *Systematic Biology* 44: 482–500.

WIKSTRÖM, J.E. 1818. Granskning af de till Thymelaearum växtordning hörande slägten och arten. *Kongliga vetenskaps academiens handlingar* 1818: 263–355.

WIJNANDS, D.O. 1983. *The botany of the Commelins*. Balkema, Rotterdam.

WILLDENOW, C.L. 1799. *Species plantarum*, vol. 2. Nauk, Berlin.

WRIGHT, C.H. 1915. Thymelaeaceae. *Flora capensis* 5, 2, part 1. Reeve, London.

WRIGHT, C.H. 1925. Thymelaeaceae. *Flora capensis* 5, 2, part 4. Reeve, London.

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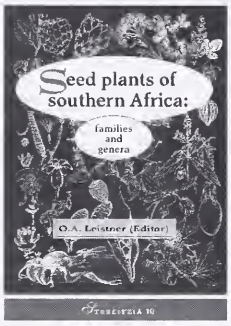

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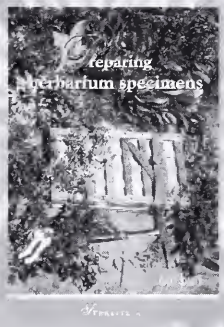

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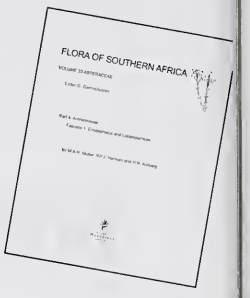

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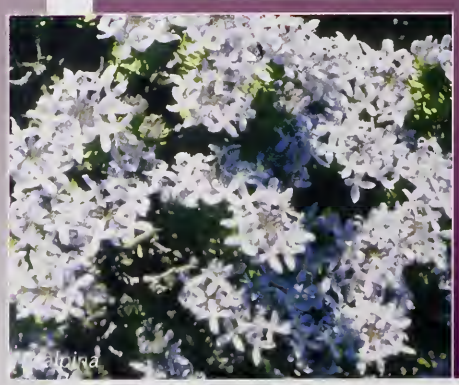
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